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THE PATHOLOGICAL RESULTS OF THE ROYAL COMMISSION ON TUBERCULOSIS.

TUBERCULOSIS is a disease which has been the subject of study from time immemorial, but it may be said that the first glimpse into the true nature of the disease was obtained when it was shown to be an infective disorder by Villemin, and the study of its nature and mode of infection first received a scientific basis through the discovery by Koch in 1882 of the infective agent : the bacillus tuberculosis. For many years the study of the disease was limited to its anatomical characteristics, both to the naked eye and to the microscope, with the result of causing great confusion in the conception of what tuberculosis really was. Indeed the large number of theories which were prevalent before the discovery of the bacillus as to what constituted the specific character of the tuberculous lesion produced nothing but chaos. The study of the anatomy of the disease, both as regards its histological nature and the distribution of the lesions in man and animals, the subject of natural tuberculosis, is, however, of great importance, and was the foundation of our clinical knowledge of the disease. But such a study is very vague and leads to erroneous conclu sions unless the mode of origin of the disease is also investigated. The study of infective diseases has this important advantage, *viz.*, that once the infective agent is known, the mode of origin, the channels of infection, and the spread of the disease in the different stages can be studied experi-

mentally in susceptible animals. Any one who has engaged in the regular performance of post-mortem examinations of either men or cattle who have died of natural tuberculosis must be aware of the difficulties surrounding an explanation of the mode in which the disease has originated. In anthrax occurring in the human being the mode of infection is, as a rule, evident in the local lesion produced at the seat of inoculation. In diphtheria and tetanus the site of infection is also evident; in the former by the false membrane which is formed by the growth of the bacillus ; in the latter, in the majority of cases, by the wound which precedes the development of the disease. These three diseases are acute. They differ from one another in the fact that, whereas in anthrax the bacillus invades the tissues and organs of the body, in diphtheria and tetanus it is localised to the seat of infection, and the symptoms and effects of the disease result chiefly in the absorption of the chemical products of the bacillus from the seat of infection. In tuberculosis, on the other hand, we have a chronic disease which may become localised, or may spread to different tissues and organs of the body, the lesions produced in the different parts being characterised by the growth of the bacillus at the particular spot. Although tuberculosis, therefore, may become a generalised disease, the infective agent is not present in the blood or fluids bathing the tissues, except as an exceptional occurrence.

The mode of infection in tuberculosis becomes from these considerations a very important study. In many instances it cannot, as has been already stated, be satisfactorily made out from a post-mortem examination of human beings dying from the disease, inasmuch as frequently at death the channel of infection is obscured by the presence of very extensive tuberculosis. Indeed it may be said that a large collection of cases of post-mortem examinations of tuberculosis in man, recorded with care from the point of view of the channel of infection, is entirely wanting. Considerable light is thrown on natural tuberculosis by the results obtained from experiment.

The channels by which infection occurs in tuberculosis,

together with the distribution of the lesions at varying dates after infection, will form the subject of the present article.

The two great channels by which infection occurs are provided in the respiratory and the alimentary tracts. In many cases of the natural disease the results of a post-mortem examination show that one or other mode of infection has occurred. Thus in the ordinary cases of chronic pulmonary tuberculosis, the stages of the disease—old at the apex, more recent in the lower parts of the lungs, with the absence or scarcity of tuberculous lesions elsewhere—show that the mode of infection has been by means of the lungs. Also, where there is primary tuberculosis of the intestines or peritoneum and a second more recent tuberculosis of other parts of the body, it is evident that infection has taken place by means of the intestinal tract. But there are very numerous cases of tuberculosis which are by no means so simple as this; there are, for example, cases in which both lungs and intestines are affected; where there is no lesion in the lungs or intestines, that is, at the site of infection; and, thirdly, where the local lesion at the site of infection is out of all proportion to the tuberculosis which subsequently develops. It is on these two last points that I would lay special stress, namely, the absence of the local lesion at the site of infection and the disproportion between the tuberculosis of the body and the size of the local lesion.

The importance of these two points is brought out by the results obtained in the experiments made for the Royal Commission on Tuberculosis.

In experimental tuberculosis (and indeed in natural tuberculosis) the severity of the disease—that is, its acuteness and its generalisation—depends on three factors: the dose of the virus, the vital activity of the bacilli in the infective material used, and the resistance or refractoriness of the animal used for experiment. The last point is one which is controllable by experiment, inasmuch as if an animal susceptible to the disease is chosen for experiment, and the results compared with those obtained in more refractory animals, the resistance to the disease can be estimated with

a degree of exactitude which is quite impossible in man. In the experiments of which I shall speak three classes of animals were used : guinea-pigs, pigs and calves. Guinea-pigs are extremely susceptible to the disease, which in them never undergoes the more advanced retrogressive changes, such as the extensive fibrosis and calcification which are observed in men and cattle. A small dose is sufficient to infect, and the disease progresses under certain circumstances until all the glands and organs of the body are affected. Pigs and calves vary somewhat in their resistance to the disease, according to the breed.

It is difficult in any tuberculous material obtained from cattle to estimate the varying activity of the bacillus present, but for several reasons which will be adduced, in the experiments with meat and milk which will be discussed, the activity of the bacillus is not a point which can be considered as of great importance, inasmuch as the effect produced appeared to be proportionate to the dose given. In acute specific diseases the dose of the virus bears some relation to the severity of the disease ; this is much more so, however, in chronic tuberculosis, where, owing to the slow formation of the lesions, the more bacilli present the more lesions result. For this and other reasons which are more fully discussed in the report of the experiments, the varying effect which will be described in experiments with meat and milk, is more a question of dose than of any other factor, so that virulence of the virus in these experiments is practically equivalent to a large dose ; non-virulence, to a small dose.

The infective material which was used in experiments was bovine tuberculous material, obtained from the organs of tuberculous cattle; sputum from cases of human tuberculosis ; and meat and milk from tuberculous cattle. As regards meat, it may be said that the experiments showed that its infectivity depended not so much on the presence of tuberculous lesions in the muscular tissue as on the contamination of the meat during its removal from the carcase, so that the infectivity of the meat was sometimes great and sometimes slight, being dependent on the amount of smeary tuberculous material which accidentally contaminated it. Milk was

found infective only when the udder was the seat of tuberculosis, and was highly infective in those cases in which tubercle bacilli were readily discoverable by microscopical examination, but was less infective when the bacilli were with difficulty found, or were not found at all, although the results of experiment showed that they were present.

If a large dose of tuberculous material, bovine or human, is introduced under the skin of the groin of the guinea-pig, a local lesion is produced in from seven to ten days, and a subsequent infection of the inguinal glands occurs ; in fourteen to twenty days an affection of the lumbar and cœliac glands, followed by a spread of the disease to the posterior mediastinal and bronchial glands, and to the lungs ; this occurs in about the fourth or fifth week. Subsequently the cervical glands, the anterior mediastinal, and even the mesenteric glands may be affected ; while the liver and spleen are affected in about the same time as the cœliac glands, that is, in about three weeks. There is, therefore, after inoculation in the guinea-pig, a gradual spread of the disease along the lymphatic channels ; from inoculation, a local lesion of the mucous membrane of the intestine never results. This rapid spread of the disease is, however, not seen in some cases of inoculation with meat and milk, in which the infectivity is slight. In these cases—several of which were observed—even when the animal was inoculated in both groins, tuberculosis developed on one side only ; also in some instances the disease remained quite localised. In one guinea-pig, for example, inoculated in each groin with meat, and dying in sixty-two days, the right inguinal region was normal, but in the left inguinal region a small scar was found inside the nipple, which, on microscopical examination, showed a structure closely resembling that of lupus, and the presence of a small number of tubercle bacilli. No other gland or organ of the body was affected by the disease. Similar localisation of the disease to the inguinal region was found in three other experiments in rabbits inoculated with meat or meat juice and killed in 66, 85, and 120 days after inoculation. The lesions were tubercular, as shown by their structure and the presence of

tubercle bacilli, and the localisation of the disease must be ascribed to the smallness of the dose given, inasmuch as in some of the other animals inoculated with material from the same source a spread of the disease was exhibited. It is evident from this that the localisation of the tuberculous lesion to the seat of infection may be due to the smallness of the dose, and not solely to the resistance of the body to the invasion of the bacillus ; or, to put it in other words, the smallness of the dose enables the tissues to successfully localise the disease.

Although the results of these inoculation experiments are suggestive, they yield in interest to those which result from feeding with tuberculous material. When guinea-pigs are fed with virulent tuberculous material a local lesion in the intestines or cæcum is always developed, and a subsequent invasion of the lymphatic glands in connection with the cæcum and intestine occurs. The disease then spreads to the cœliac glands and to the liver and spleen, and subsequently to the posterior mediastinal and bronchial glands and to the lungs ; finally, all the glands in the body may be affected. The earliest time at which a local lesion was discoverable in the intestine was eighteen days, and in about six to eight weeks most of the organs of the body are affected. Here, again, in the guinea-pig there is evidence of the spread of tuberculosis along the lymphatic channels. The cases in guinea-pigs in which, after feeding, tuberculosis tended to become localised were those in which either a small dose of virulent milk was given or a dose of very slightly virulent milk. Thus, four guinea-pigs were fed during the course of two days with 200 c.c. of milk which was only slightly virulent ; one died in twenty-five days, and showed no tuberculosis ; the second, third and fourth died respectively in forty-nine, fifty-three, and sixty-seven days. These three developed tuberculosis ; but the disease was present in the intestines and mesenteric glands only in the first two, and in the mesenteric glands only in the third. In forty-nine days, when virulent milk was given, the disease had usually extended to the liver and spleen and the lymphatic glands of the body. The case of the third animal,

which showed no local lesion of the intestine, is of great interest, as showing that when the material was non-virulent the bacilli could pass through the mesenteric glands without producing a local lesion. This point is further emphasised by the experiments on pigs.

Pigs are the subject of natural tuberculosis, which is, in the great majority of instances, due to the eating of tuberculous material. As an example of natural tuberculosis of a severe type resulting from the ingestion of tuberculous material the following case may be quoted. There was a large tuberculous ulcer of the right tonsil and tuberculosis of the corresponding lymphatic gland below the jaw; this was connected with a chain of tuberculous glands on the right side of the neck. There were several recent tubercular ulcers in the cæcum, but none in the intestines, and the cæcal and mesenteric glands were extensively tuberculous. The cœliac glands were also affected, and those in the lesser omentum; the liver and spleen showed caseous tuberculosis. The posterior mediastinal and bronchial glands were also affected by the disease, and there was acute caseous miliary tuberculosis of the lungs, with tuberculous pleurisy and effusion of clear liquid on both sides. In this case it is evident that the sites of infection were at the right tonsil and in the cæcum. In the pig the tonsils are frequently a channel of infection of tuberculosis. From the tonsil the disease spread to the neighbouring lymphatic glands, and down the chain of cervical glands to the glands in the thorax; thence to the lungs, and from the cæcum the disease spread to the mesenteric glands, the cœliac and the glands of the lesser omentum, and the liver and spleen.

As far as could be judged, this pig had been infected about eighty days before it was slaughtered.

A second case of tuberculosis in the pig, resulting from feeding with virulent tuberculous material, may be quoted. A healthy pig was fed with 120 grammes of bovine tuberculous material, and was killed in fifty-seven days. There was found one tuberculous ulcer in the small intestine, which measured one-quarter of an inch by one-half. Several

of the mesenteric glands were affected, and from these the disease spread to the glands of the lesser omentum, to the liver and spleen, to the posterior mediastinal glands, and finally to the lungs, which were the seat of caseating miliary tuberculosis. This case is instructive, inasmuch as it reproduces, almost exactly, some of the cases of feeding tuberculosis occurring naturally in human beings. The local lesion of the intestine is out of all proportion to the tuberculosis resulting in the rest of the body, and especially in the lungs. In children such cases are not infrequently seen, and indeed the ulcer in the intestine may heal, or the mesenteric glands become calcareous, so that unless carefully examined the disease may appear as one of primary lung tuberculosis.

The results of feeding pigs with non-virulent tuberculous material, namely, with meat and milk, may now be considered. The first case was that of a pig fed with twelve litres of slightly virulent tuberculous milk. It was killed in sixty-eight days, and tuberculosis of the mesenteric glands alone was found. There was no local lesion in any part of the alimentary tract, and no affection of any gland or organs other than the mesenteric glands.

In another case a pig was fed with about four kilograms of meat from a tuberculous cow, and was killed in 106 days. In this case also there was no lesion in any part of the alimentary tract, but the cœliac glands were tuberculous, as well as the lymphatic glands on the right side below the angle of the jaw, and both the liver and spleen showed scattered nodules of caseous tubercle. All the other organs and glands of the body were normal. The channels of infection in this case were, therefore, through the right tonsil into the neighbouring lymphatic gland and through the upper part of the intestines into the cœliac glands, from which the liver and spleen were affected.

The third case occurred in a pig fed with 1190 grams of meat from a tuberculous cow. It was killed in 203 days, and, as in the other two cases, there was no local lesion in any part of the alimentary tract. The cœliac glands and those in the lesser omentum were tuberculous, as well as the

posterior mediastinal and the bronchial glands, while one epididymis showed a tuberculous nodule. The channel of infection here was, therefore, through the upper intestinal tract into the cœliac glands, and thence to the posterior mediastinal and bronchial glands, while the interest of the result depends on the fact that a part of the body (that is the epididymis) far removed from the seat of infection became tuberculous. While, therefore, as in the other cases, the part first affected was the lymphatic glands, the affection of the epididymis can only be ascribed to a conveyance by the blood stream of the tubercular virus.

The results obtained by feeding calves with tuberculous material illustrate some of the important points in the distribution of tuberculous lesions which occur in the human being. In the calf and cow the intestinal lesion which results from feeding with tuberculous material frequently does not ulcerate, caseous nodules being formed in the Peyer's patches, which may undergo calcification, or may even heal. This was several times observed in natural tuberculosis in the cow. Ulceration may also take place. Four calves were fed with one kilogram of bovine tuberculous material, namely, minced lung, lymphatic gland and udder, all extensively diseased. The calves fed out of the same trough and were kept in the same shed. The first calf was killed in twenty-eight days and showed 116 caseous nodules in the Peyer's patches of the small intestine, and affection of the corresponding mesenteric glands, but of no other organ or gland in the abdomen. In the thorax, the bronchial glands were affected, and there were a few scattered tubercles in the lung tissue near the surface. Here, then, the seat of the infection was the small intestine, from which the mesenteric glands were affected, and subsequently the bronchial glands, the intervening lymphatic glands being skipped by the disease.

The second calf was killed in sixty-one days. Sixteen nodules of tubercle were found in the intestine; a few of the mesenteric glands were tuberculous, and, as in the other calf, the remaining abdominal glands were skipped, and the posterior mediastinal glands were affected, the bronchial

glands and a few of the lower cervical glands, while there were a few nodules in the lungs.

The third calf was killed in eighty-five days and showed numerous superficial ulcers, especially in the lower part of the ileum and in the cæcum, while the cæcal and mesenteric glands were also affected, and the posterior mediastinal and lower cervical glands were tuberculous. The lungs showed a few nodules of tubercle, and the lower part of the pleuræ showed the characteristic "grapes" of bovine tuberculosis. The last calf was killed in 259 days. Twenty-five nodules were found in the small intestine, and there was tuberculosis of the mesenteric glands and of a few of the retro-hepatic glands, while the posterior mediastinal and the bronchial glands were tuberculous, and the glands below the angle of the jaw on the right side. Besides this there was extensive tuberculous pleurisy in the form of "grapes," the lung tissue itself being unaffected. In the three first calves the channel of infection was through the intestinal tract, and thence it affected the mesenteric glands and subsequently the glands and organs in the thorax. This was frequently observed also in natural tuberculosis in cattle, namely, that from the seat of the infection in the intestine the organs and the thorax are soon affected. In the fourth calf the seat of infection was two-fold: in the small intestine and in the pharynx on the right side. The results in this calf are interesting, as showing that tubercular pleurisy can occur from intestinal infection without the lung tissue itself being involved. The results, therefore, of the feeding of pigs and calves with tuberculous material, show three chief points, namely, that with a small dose there may be absence of a local lesion at the seat of infection; that the neighbouring lymphatic glands are almost constantly affected; and that the size of the local lesion may be out of all proportion to the tuberculosis which subsequently develops.

These results are to some extent explanatory of the cases of tuberculosis which occur in the human being. A few of these may now be referred to. It is seen, both in the pig and calf, that the glands below the jaw are readily affected, especially in the pig, by the ingestion of tubercu-

lous material, even though this may be slightly virulent in nature, and this affection through the pharynx occurs without the production of a local lesion and reproduces what are known as scrofulous glands in the neck of human beings. It is also seen that from these tuberculous glands below the jaw the disease in some instances spreads down the cervical glands and affects the lungs by way of the bronchial glands: an exact reproduction of some cases of pulmonary tuberculosis in the human being. The proportion of cases in the human being in which intestinal infection occurs is probably greatly under-estimated, and the results of post-mortem examinations are frequently misread, owing to the fact that extensive disease in the lungs leads us to the conclusion that the disease was primary there, the lesion in the intestine being very slight. As regards the infection of the lungs in the human being, it may be ascribed to four modes of infection. When primary, it is due to inhalation of tuberculous material in a dried state; when secondary, it may spread downwards from the primary affection of the glands below the jaw; thirdly, it may spread upwards from the intestines without affection of the intervening glands; and, fourthly, it may occur from the presence of an active focus elsewhere, either in a joint or bone.

Tuberculosis of the lymphatic glands in the thorax, the bronchial and posterior mediastinal glands, is not an uncommon affection in children. Experiment appears to show that the commonest modes of infection are either from scrofulous glands in the neck or from the intestines, and, as in the experiments on the calf, the lesion in the intestine may be slight and the lesion in the thorax great. It is possible, however, that the bronchial glands might be affected by the inhalation of a small dose of tuberculous material through the lung itself, no local lesion in the lung tissue being produced. This, however, is purely theoretical, since I am not aware of any experiments in which the inhalation of small quantities of tuberculous material has produced this effect.

As regards the other lesions in the human being which result from intestinal infection, the chief of which is tuber-

cular peritonitis, it must be remembered that the form of tubercular peritonitis that occurs in children does not exist in guinea-pigs, cattle, or pigs. It is present in horses. In human tubercular peritonitis in some cases a local lesion is found in the intestine ; in other cases there is no local lesion ; the mesenteric glands are tuberculous, and the chief seat of the disease is the peritoneum. It seems very probable that in many cases of tubercular peritonitis the affection is associated with the ingestion of a small dose of the tubercular poison, although this is not so in all cases.

Affection of parts of the body far removed from the channel of infection (such, for example, as the bones, joints, the epididymis, and the pia mater) is one of the most interesting problems in tuberculosis ; since there is no direct lymphatic connection between these parts, and from the primary tubercular lesion infection must occur by means of the vascular system. Thus in the human being tubercular joint or bone disease, or infection of the epididymis or the pia mater, may occur in a case which is evidently primary lung tuberculosis, or primary intestinal tuberculosis. But there are other cases in which the channel of infection is not so evident. In some of these, indeed, a tubercular lesion in the retrograde stage is present at the apex of one or other lung, or in the intestine, or is shown in scrofulous glands below the neck, or in tuberculosis of the mesenteric glands. These small lesions are frequently overlooked in post-mortem examinations, so that the cases are described as primary tubercular meningitis, epididymitis, or bone, or joint disease. In some cases, however, the primary local lesion cannot be discovered, although it is more frequently not looked for, and it is quite possible that in the tissues of children, which are so active in absorption, the tubercle bacillus might enter the blood stream directly without producing a local lesion, and so be carried to a distant part, where it produces its characteristic lesion.

The exigencies of space preclude a further discussion of this part of the subject, and I will finish what I have to say by considering briefly some of the sources of infection in tuberculosis. If tuberculosis is a disease in which an

attempt has to be made to diminish its prevalence, it is evident that a correct appreciation of the sources of infection is of the highest importance. These sources are either the discharges or secretions of tuberculous organs, or tuberculous lesions removed in cases of natural tuberculosis in man or animals. Of the first class sputum and milk are the chief. It is probable that to milk derived from tuberculous cattle is to be ascribed the majority of cases of ingestion tuberculosis that occur in children. To sputum in the dried state most of the cases of primary lung tuberculosis must be ascribed. Tuberculous organs in cattle, when given to animals as food, will tend to perpetuate the disease. The meat of tuberculous cattle, when no care is taken in its "dressing" to prevent contamination with tuberculous material, is also a source of infection, and the discharges from tuberculous cattle kept in stalls leads to the infection of healthy cows present in the same shed. By proper regulations made by the State the danger from milk and meat could be diminished, or even completely eliminated; and the individual, by always boiling milk and by properly cooking the meat, can reduce the danger of infection to a minimum. With sputum, however, the case is different. No State regulations are here available, inasmuch as if they were made they would probably be more frequently infringed than followed. The duty of the medical profession seems to be to instruct tuberculous patients under their charge that their expectoration is of danger not only to themselves, but to those surrounding them; that it is infective material which ought to be destroyed and which is destroyed with very little trouble to themselves. By educating the people in this manner a large amount of tuberculous material which is a source of danger to the community will be destroyed, and, combined with proper regulation of the milk and meat supply, will undoubtedly in time tend to diminish the present scourge of tuberculosis.

SIDNEY MARTIN.

PITHECANTHROPUS ERECTUS—A BRIEF REVIEW OF HUMAN FOSSIL REMAINS.

1. INTRODUCTORY.

WHEN Darwin published, in 1871, *The Descent of Man*, the impression was general that he had solved and settled the genealogy of Man. Our modest master, however, made no such pretension; he claimed no more than to have enunciated Man's descent as a problem, and to have brought it within the arena of practical science for a solution. Within that arena the problem still remains. In 1895 no more is known of how the histories of man, the gorilla, the chimpanzee, the orang and the gibbon, twined together in the past than in 1871. At that time it was thought that a close study of the animals themselves would reveal their histories. Embryology was expected to yield a great deal. The embryo, it was believed, recapitulated its own history as it unfolded itself, but the good deal we know of the human embryo, and the very little we know of the simian, have taken that hope from us. Vestigial structures, also, were regarded as a kind of genealogical finger-posts, but their indication has proved to be so indefinite as to suggest that they are rather "weather-cocks" to the wind of many theories. Evidence of the line of descent, yielded by anatomical structure, is of a general nature only. Even were we in a position to say that Man and *this* animal have 60 per cent., and that Man and *that* animal have 70 per cent., of characters in common—a position we have not nearly attained—we were no nearer the solution of his descent. All that such knowledge permits us to say is that man is a primate of the Primates, a catarrhine of the Catarrhini. But the strong hope remains that one source of certain evidence is left us. We hope that, as the primate stock broke up in the past, and came struggling into the various human and anthropoid forms of to-day, Time turned down some stray specimens in his geological pages, and thus preserved their histories in

unequivocal characters. The evidence derived from this source can, as far as it yet concerns man's descent, be compressed within the bounds of a moderate article.

2. THE BENGAWAN FIND—THE LATEST ADDITION TO THE HUMAN GEOLOGICAL RECORD.

The latest page has been opened in Java by Dr. Eugene Dubois, and has yielded us a calvaria, a tooth and a femur supposed to belong to an individual that flourished in an early post-tertiary period.[1] In the hills near the centre of the long island of Java the Bengawan takes its rise, and then runs its short course northwards to the sea. Some parts of the district drained by this stream have yielded fossil remains of animals believed, by their finder, Dr. Dubois, to belong to Pleistocene times, and while extending his researches on the left bank of the Bengawan, he unearthed the tooth and skull one metre apart, the femur fifteen metres farther up stream, and all at the same depth —one metre below the level of the bed of the Bengawan. That is, practically, all he tells of the circumstances in which these remains were found. The mere fact that they were found in the bank of a stream—which, like all tropical streams, must play great havoc with its course during the rainy season—inclines us to doubt, until Dr. Dubois can inform us to the contrary, the possibility of assigning them, at present, their correct geological age. For me, the proof of their antiquity lies in the peculiarity of their conformation.

Given the roof of a cranium, sliced off at the level of the supra-orbital ridges, an upper third molar tooth of large size and peculiar form, and a femur almost entire: reconstruct the animal or animals to which they belonged. This was the task that confronted Dr. Dubois, and the result we have in a rather extensive memoir[2] issued from the Batavian press towards the close of last year. He met

[1] *Cf.* footnote on p. 368.

[2] Pithecanthropus Erectus. *Eine Menschenæhnliche Uebergangsform aus Java*, Batavia, 1894, 39 pp., 4°, 2 pls. Full lists of references are given.

it in the usual way; he compared these remains with the corresponding parts of the chimpanzee, gorilla, orang, gibbon and Man, and found in neither one nor another the agreement he sought for. He made no allowance, however, for the extraordinary amount of individual variation manifested by men and anthropoids, and concluded that these remains were parts of an animal that had shared human and simian characters almost equally. To this extinct animal he gave the name *Pithecanthropus Erectus*, believing it to represent a family that flourished in Pleistocene times. At the meeting of the Anatomical Society of Great Britain and Ireland, held on the 13th of February last, Professor Cunningham[1] brought the Bengawan find under discussion, and showed that the calvaria was in all respects human, and assigned it to a race of men even more primitive than the Canstadt to which the celebrated Neanderthal skull belongs. The tooth he also regarded as human, and as belonging, probably, to the same individual as the skull; but the femur he rejected as that of a recent and modern human being. Independently, M. Pettit[2] arrived at an almost similar conclusion. A reviewer[3] of Dr. Dubois' memoir, on the other hand, while entirely accepting the Bengawan remains as human, assigned them to a modern but abnormally microcephalic specimen of the existing race. At the meeting of the Anatomical Society[4] I adduced some reasons for believing the tooth to be that of an orang, and the skull that of an atypical member of the human race. But much extended research has led me to see that my reasons were not well founded, and that Cunningham and Pettit are very probably right in regarding these remains as indicative of a human race more primitive than any hitherto discovered.[5]

[1] See also *Nature*, 28th Feb., 1895, p. 428.

[2] *L'Anthropologie*, tom. v., 1895, pp. 65-69.

[3] *Nature*, 24th Jan., 1895, p. 291.

[4] *Proc. Anat. Soc. Great Britain and Ireland*, 13th Feb., 1895.

[5] After this article was in proof, Sir William Turner made an important contribution to the literature over the Bengawan remains (*Journ. Anat. and Physiolog.*, April, 1895). He gives a full description of the calvaria; and

History repeats itself.[1] When Fulhrott, in 1857, brought forth the Neanderthal calvaria[2] from the Feldhofer cave, nearly as many speculations arose concerning the nature of the individual to which it belonged as there were anthropologists in Europe.

Fuhlrott, Schaaffhausen, Huxley, Broca, Hamy and Busk regarded it as representative of the men that inhabited Western Europe with the mammoth and woolly rhinoceros; Virchow decided that it had been subjected to pathological processes, and was therefore unfit for grounds of inference; Barnard Davis inclined to a similar opinion; Pruner Bey thought that it was part of an idiot's skull; Turner pointed out that an approximately similar type of calvariæ occurred occasionally in modern European skulls; R. Wagner instanced skulls of modern Dutchmen that closely resembled the Neanderthal; Meyer set it down as the skull of a Cossack who had perished in the wars; and King regarded it as the calvaria of an extinct pithecoid animal. It is unnecessary to cite the sources of these speculations, for the discovery of the Spy crania,[3] in 1886,

as regards it, and also the femur, arrives at conclusions similar to those of Cunningham and Pettit. He infers from the figure given by Dubois that the tooth is probably that of an orang. My reasons for regarding the tooth, now, as human are, that its enamel-pattern and the condition of its oblique ridge occur in the wisdom teeth of some negroid races, but not, so far as I have seen, in the teeth of the orang. Dubois' figure is, however, not very clearly delineated.

[1] *Kritische Bedenken gegen den Pithecanthropus Erectus. Globus*, B. lxvii., No. 14, by Dr. Rud. Martin, Docent d. Anthropologie, Zurich. He is of opinion that the Bengawan remains are human, but too fragmentary to permit inference as to the animal of which they formed part. I am obliged to Professor Cunningham for the opportunity of seeing Dr. Martin's contribution.

[2] Of the very extensive literature called forth by the Neanderthal Find, the contributions which best repay consultations are Schaaffhausen's *Der Neanderthal Fund*, Bonn, 1888; Huxley's *Evidence as to Man's Place in Nature*, London, 1863 (see also in Lyell's *The Antiquity of Man*, 4th ed., 1873); Virchow's *Untersuchung des Neanderthal Schädels, Zeitschr. für Ethnologie*, 1872; Turner's *Quart. Journ. of Science*, vol. i., 1864, pp. 250-558.

[3] Fraipont et Lohest, *Le Race Humaine de Neanderthal ou de Canstadt en Belgique*, Gand, 1887, 8°, pp. 153, 4 pls. with 21 figs. To

has set the matter at rest by confirming the deductions of Schaaffhausen, Huxley and Broca as to the nature and antiquity of the Neanderthal skull and race. I am convinced that the promulgation of so many and so various theories has been largely due to an under-estimation of the variation in structure amongst individual men and anthropoids, and to an exaggeration of the structural interval that separates these two groups of primates.

3. AN ENUMERATION OF THE PRINCIPAL FINDS OF FOSSIL MAN.

The south-eastern provinces of Belgium have proved so far to be the chief graveyard of Quaternary man, the finds made in France, Italy, Germany and England[1] being merely corroboratory items. These provinces offered suitable conditions for the preservation of remains. Through this part of Belgium run the Meuse and its many tributaries, frequently confined between bluffs of Devonian limestone. On the faces of these bluffs, fifteen to thirty metres above the present stream-levels, open caves which were frequented by man, the cave bear, the cave hyæna, the mammoth, the woolly rhinoceros and other members of the fauna of Western Europe during Quaternary times. Any bones left on the floor of the cave tended, in the course of time, to become buried by the constant stalagmitic droppings, the surface soil washed in through vents in the roof, and now and again by the addition of fragments of limestone detached from the vault. Disintegration of the surface of

this work I beg to acknowledge my indebtedness. A masterly description of the Spy remains is given, along with a clear and brief account of former similar discoveries.

[1] Professor Howes has drawn my attention to the most recent and evidently most important find of this nature yet made in England. ("On a Human Skull and Limb-Bones found in the Palæolithic Terrace-Gravels at Galley Hill, Kent," by E. T. Newton, F.R.S., *Proc. Geo. Soc. Lond.*, May 22, 1895.) The find, as such finds go, is very complete. The brain-chamber of the skull evidently differs considerably from that of the Spy crania, but, on the other hand, its teeth and facial parts closely agree. Mr. Newton intends to publish a more detailed account of these remains.

the bluff led to a gradual exposure of the cavern floor as a terrace in front of the mouth. From this formation Schmerling took the Engis remains;[1] Fuhlrott, in 1857, the Neanderthal; Dupont,[2] in 1865, the Naulette; lastly, Lohest[3] and De Puydt, in 1886, the Spy remains—the most complete and valuable of all.

All fossil human remains hitherto discovered could be placed within a museum cupboard of very limited dimensions. Skulls would be represented by the nearly complete arches of Spy crania Nos. 1 and 2; the Engis[4] cranial vault; the roof caps of the Bengawan, Neanderthal, Tilbury,[5] Staegenaes and Forbes Quarry (Gibraltar) crania; and the partial calvaria of the Brux,[6] Denise, Canstadt, Eguisheim, Olmo and Clichy discoveries. Facial parts would be represented only by the fragmentary upper jaw and malar of Spy cranium No. 1. Only two lower jaws of importance, and lacking the greater parts of the ascending rami, would be present—those of the Naulette and Spy cranium No. 1. The fragments of the Schipka,[7] Goyet, D'Arcy-sur-Cure and Clichy mandibles would add very little to our knowledge of these two; while the Tilbury, Suffolk[8] and Moulin Quignon inferior maxillæ, even were their claims to antiquity allowed, would be of little value, for they are the mandibles of aged individuals and consequently their characteristics have been erased by age-changes. The cupboard would contain about sixty-two teeth, twenty-two

[1] Schmerling, *Recherches sur les ossemens fossils découverts dans les cavernes de la Province de Liège*, Liège, 1846. Text and atlas (75 pls.).

[2] *Bull. de l'Acad. de Bruxelles*, 2nd ser., t. xxii., 1866, pp. 31-55.

[3] Fraipont et Lohest, Gand, 1887.

[4] See Huxley's *Evidence as to Man's Place in Nature*, London, 1863.

[5] Owen, *The Antiquity of Man*, London, 1884, 31 pp., 4 pls.

[6] It is unnecessary to give references to the original sources where these new fragmentary crania are described, as they are of no value for our present purpose. Fraipont gives them.

[7] Virchow, *Das Kiefer aus der Schipka-Höhle und das Kiefer von Naulette, Zeitschrift für Ethnologie*, bd. xiv., 1882, pp. 276-310.

[8] Robert H. Collyer, *Anthropological Review*, vol. v., 1867, pp. 221-235.

of the upper jaw and forty of the lower, belonging to the Engis, Naulette, Schipka, Spy, Tilbury and Bengawan finds. The bones of the limbs, none of them complete, would be represented by about eight femora, three tibiæ, fragments of fibulæ, eight humeri, seven parts of forearm bones, and fragmentary parts of clavicles, ribs, vertebræ, hand and foot bones, and a few pieces of scapulæ and ilii. These fragments represent altogether little more than a score of the men that flourished in the Quaternary period, and of these fragments only those of the Neanderthal, Spy and Bengawan finds are of value for purposes of reconstruction. Only four individuals to represent the millions and millions of men that must have lived and died in Quaternary times!

4. FOSSIL SKULLS AS BRAIN CASES.

The first and prime function of a skull is to carry the brain, and this office, fossil skulls served but moderately well. The cranial capacities of 100 modern Parisians[1] were found to fluctuate between 1150 c.c. and 1850 c.c. Turner found that thirty Australian crania, gathered at random during the *Challenger* Expedition, possessed cranial capacities ranging from 930 c.c. to 1514 c.c.[2] The cranial capacity of the Bengawan skull is roughly estimated at 1000 c.c.; the Neanderthal skull at 1230 c.c., by Huxley;[3] 1100 c.c., by Schaaffhausen;[4] and the Spy crania at about 1300 c.c. In thirty orang skulls I have found the cranial capacity to range from 300 c.c. to 530 c.c., and in other anthropoids an equally great variation in brain capacity. We have every reason to believe that the cranial capacities of fossil man showed a variation in brain capacity equal to that of modern man, so that we accept very reservedly the cranial

[1] Topinard, *Eléments d'Anthropologie Générale*, Paris, 1885.

[2] "Report on the Human Crania and other Bones of the Skeleton Collected during the Voyage of H.M.S. *Challenger*," "*Challenger*" *Reports*, pt. xxix., 1884 (Crania); pt. xlvii., 1886 (Skeleton).

[3] *Evidence as to Man's Place in Nature.*

[4] *Der Neanderthal Fund*, Bonn, 1888, 49 pp., 19 figs.

capacities of the Bengawan, Neanderthal and Spy individuals as representative of Quaternary man.[1]

Thirteen hundred cubic centimetres contained in the short, narrow and high cranial chambers of modern Europeans are no better than, as far as we know, an equal number contained in the elongated, wide and depressed skulls of fossil men. The fact remains, however, that, since Quaternary times, the prevalent form of brain chamber has changed. The lengths of Bengawan, Neanderthal and Spy cranial chambers are 155, 169, 168, 170 m.m.; the greatest breadths, 120, 135, 130, 140 m.m.; basi-bregmatic heights, 110 (?), 125 (?), 128, 132 m.m. In these diameters they resemble a considerable proportion of Australian crania, except that the fossil skulls are relatively broader than their existing counterparts. In the majority of modern Europeans the length and breadth, as compared with fossil skulls, have been sacrificed for an addition to the height of the cranial chamber; but occasionally forms occur with diameters that approximate to those of the Australian and fossil crania. In this we see how gradually the type changes. The squat, low-browed crania were evidently the prevailing forms in Quaternary times; they have come straggling down to the present in ever-diminishing numbers, until they are now almost ousted by the prevalent high-foreheaded types of modern times.

In this connection the Engis skull is interesting; it has every claim to geological antiquity possessed by the Neanderthal calvaria, but it is strictly of the modern type. It is now the recipient of scant attention, but there is no reason why it may not be regarded as representative of a minority of the Neanderthal (Canstadt) race, just as the fossil types represent a minority of to-day. There never was, nor ever will be, a race that manifests more than a proportion of crania of a similar type. It is no explanation to say that divergences of cranial form are due to a mixture

[1] Turner (*Jour. Anat. and Physiolog.*, April, 1895) refers to a Quaternary skull described by Testut (*Bulletin de la Soc. d'Anthrop. de Lyon*, viii., 1889), the cranial capacity of which is estimated at 1700 c.c. The original communication I have not been able to consult.

of races. There never was, nor ever will be, a pure race; love and war have kept, and will keep, races constantly mixing.

5. THE SKULL OF FOSSIL MAN CONSIDERED AS A MASTICATORY APPARATUS.

We may accept the size of the palate as an indication of the degree to which the masticatory and alimentary systems of fossil men were developed. We have only an upper wisdom tooth to give us a clue to the Bengawan palate, and we may infer that a set of teeth, such as the Bengawan molar from its size and shape indicates, could not be set in a palate less than 70 m.m. wide and 60 m.m. long. The alveolar outlines of the lower jaws permit us to infer that the palate in one of the Spy crania (supposed to be that of a woman) was about 60 m.m. broad and 54 m.m. long, and in the Naulette individual 65 m.m. broad and about 62 m.m. long. In eight Australian crania of a type resembling the fossil forms, the palates ranged in length from 55 to 64 m.m., the breadth from 60 to 72 m.m., the one diameter commonly increases as the other diminishes. In English palates 52 m.m. long and 56 m.m. broad are quite common diameters. Amongst gorillas the palate frequently measures 95 m.m. in length by 66 m.m. in breadth; amongst chimpanzees 82 × 61 m.m.; and amongst orangs 94 × 70 m.m. From these figures it is quite plain that the palatal areas of fossil man and certain Australians are greater than the palatal areas of most modern men; while, on the other hand, the palates of anthropoids greatly exceed those of fossil men. The brain capacities, on the contrary, are greatest in modern man and least in anthropoids. An increase of the cranial capacity appears to determine a diminution of the palatal area. An increase of brain capacity indicates an increased power of bringing more easily masticated food within the reach of the individual, such as may favour a reduction of the palate, masticatory and alimentary apparatuses, with profit to the body—economy.

The principle of the evolutionary progress of human structure appears to lie in an increase of brain capacity,

and, as far as is profitable, a diminution of the alimentary apparatus. Further, we may infer that a man, or an anthropoid, with a small brain and a large masticatory apparatus is an approach towards the primitive primate stock that gave them birth. Judged on this standard, the Bengawan and Neanderthal individuals may be set down as distinct human approximations to the primate stock.

6. OTHER MODIFICATIONS OF THE HUMAN FOSSIL SKULLS ENTAILED BY A LARGE MASTICATORY APPARATUS.

The prominent supra-orbital ridges of the fossil crania form one of their most characteristic features. The thickness of the skull over the glabellar (supra-nasal) part of these ridges measures in the Bengawan, Neanderthal and Spy crania from 24 to 30 m.m., the describers failing to give us more exact figures. Australian crania of the cynocephalic type show frequently an almost equal glabellar thickness. In modern European skulls the measurement seldom exceeds 20 m.m. In gorilla skulls the glabellar part measures, in thickness, from 30 to 35 m.m.; in the chimpanzee from 25 to 28 m.m.; in the orang from 16 to 20 m.m.; and in the gibbon from 12 to 14 m.m. In fossil and most cynocephalic Australian skulls, as well as in those of the gorilla, chimpanzee and gibbon, the glabellar part of the supra-orbital ridge is as prominent as the supra-ciliary parts. In the orang and in the Tilbury skull the supra-ciliary parts are separated by a glabellar hiatus; and in modern skulls the glabellar part is extremely variable, being often present and prominent in men, and often absent in women. There can be little doubt that the main end of this supra-orbital bar is to strengthen the encasement of the face, and provide a more extensive cranial basis for the large masticatory apparatus; hence its large size in anthropoid and fossil human skulls. Its development may in some degree be dependent also upon sexual elements, for it is commonly larger in the male than in the female, in whom it frequently begins to grow when the child-bearing period is past. The prominence of the supra-orbital ridges is due, according to

Fraipont, to the size of the facial muscles. Carus,[1] on the other hand, thought they were most strongly developed in animals of keen sight.

Much has been made of the frontal sinuses that inflate the supra-orbital ridges, and are very large in the fossil skulls. Huxley[2] cited evidence showing them to be correlated with the respiratory apparatus. Others have thought them correlated with the sense of smell. The frontal sinuses are, however, in nowise different from those of the maxillary, sphenoid, ethmoid and mastoid bones, which are merely economical methods of gaining an increase of bulk and surface with no increase of weight.

The supra-orbital ridges terminate laterally in the external angular processes, which, in the fossil skulls, are extremely prominent. This process in the Bengawan skull measures 18 m.m.; in the Neanderthal, 24 m.m.; in Spy cranium No. 1, 16 m.m.; in Spy cranium No. 2, 14 m.m.; in Cynocephalic Australian skulls, from 12 to 20 m.m.; in the modern European, from 8 to 14 m.m.; in the gorilla, about 40 m.m.; in the chimpanzee, frequently 30 m.m.; in the orang, about 33 m.m.; and in the Siamang, about 22 m.m. The malar part of the temporal muscle takes its origin from this process, so that its prominence in human fossil skulls indicates for us the high degree to which the malar part of the temporal muscle was developed in fossil man—a development indicative of a heavy burden of work upon the molar teeth.

A prominent external angular process is also a simian characteristic, and probably also a feature of the ancestral primate stock.

The temporal ridges on the human fossil skulls indicate for us, by their situation on the parietal bone, and also by their prominence, the degree to which the temporal muscles were developed. The temporal ridges, bounding the temporal area of the parietal, are decipherable with difficulty in the Bengawan skull; they are easily made out, but not

[1] Quoted by Fraipont.

[2] *Evidence as to Man's Place in Nature.*

specially prominent, in the Neanderthal and Spy crania. On the anterior part of the Bengawan calvaria the temporal ridges run parallel to the upper and lower borders of the parietal, being 60 m.m. (?) from the upper border, and 50 m.m. from the lower. The position of the ridge may be stated as = $\frac{60}{50}$. The position of the Neanderthal temporal ridges is $\frac{60}{60}$; of Spy cranium No. 2, $\frac{60}{42}$; of Cynocephalic Australian, from $\frac{65}{40}$ to $\frac{55}{60}$; of modern European, from $\frac{90}{25}$ to $\frac{60}{50}$. The denominator of these fractions gives an index to the development of the temporal muscle, by indicating the extent of its origin. Its development was no greater in fossil men than in many Australians of to-day; but, on the other hand, it exceeded the temporal muscle of most modern Europeans.

To appreciate the inferential worth of the temporal ridges one must remember that their position depends upon several factors. In simian and human fœtuses the temporal muscle covers only the inferior border of the anterior part of the parietal. As the maxillary apparatus grows, the muscle ascends towards the vertex of the skull, preceded by the temporal ridges as osseous waves. The relative height to which they reach depends principally upon the extent of cranial capacity; to gain a sufficient area of origin they must ascend relatively further on skulls of a low than on those of a high cranial capacity, hence their relatively high position on fossil crania, and their complete ascent to the vertex of the skull in anthropoids. The only other factor that enters largely into the determination of the temporal ridge is the size of the canine teeth. The larger the canine teeth the greater the development and ascent of the temporal ridges; so that we may safely infer that the canine teeth of the Bengawan individual were incisiform. The size of the molar teeth determines the development of the temporal ridges only to a minor extent.

7. THE CONFIGURATION OF THE OCCIPITAL REGION OF HUMAN FOSSIL SKULLS.

In the same way as the temporal ridges indicate the extent of the temporal muscle, the occipital and mastoid ridges

show the development of the muscles that connected the head and body—the nuchal muscles. Much importance has been placed upon the form of the occipital region of the Neanderthal skull by Huxley, and on that of the Bengawan by Dubois. Unfortunately, only in Spy cranium No. 1 is the part below the occipital ridge—the nuchal part—of the squama occipitalis completely present; a fragment of the nuchal part is seen in the Bengawan and Spy crania No. 2; while in the Neanderthal skull the squama occipitalis is present only as far as the occipital ridge—the supra-nuchal part. There are two methods by which we may approximately estimate the amount of nuchal surface lost. We may infer its extent from the corresponding parts of similar skulls, or we may calculate it from the length of the fronto-parietal arch. In the skulls of anthropoids and men the squama occipitalis forms, in the large majority of individuals, about one-third of the cranial vault,[1] the frontal and parietal making up the other two-thirds; thus the length of the squama occipitalis is equal to half the fronto-parietal arch. It is rarely less than 45 per cent. of the fronto-parietal part; so that, in the Bengawan skull, the fronto-parietal arch being 220 m.m., we may calculate that the squama occipitalis measured, at any rate, 100 m.m. If so, the nuchal part of this skull—lying between the occipital foramen and crest—measured 66 m.m., as the supra-nuchal part measures only 34 m.m. Making a similar calculation for the Neanderthal skull, the fronto-parietal length of which is nearly 250 m.m., it is found that the lost nuchal surface must have extended quite 50 m.m. below the occipital crest; the supra-nuchal part which is present measures 62 m.m. In Spy cranium No. 1 the nuchal part of the squama occipitalis measures 67 m.m., the supra-nuchal 55 m.m.; in seven Cynocephalic Australian crania the supra-nuchal varied from 50 to 55 m.m., the nuchal

[1] Cleland, "An Inquiry into the Variations of the Human Skull, particularly in the Antero-posterior Direction," *Phil. Trans.*, vol. clx., 1870, pp. 117-175. Also Duckworth, "A Critical Study of the Crania of Aboriginal Australians in Cambridge Museum," *J. Anthrop. Instit.*, vol. xxiii., 1892.

from 45 to 55 m.m.; and in modern European crania the former measures from 65 to 85 m.m., the latter from 25 to 45 m.m. It is evident that, on the whole, the nuchal surface is greater in the ancient than in the modern type of skull; the nuchal muscles, also, must have been developed to a correspondingly greater extent; on the other hand, the supra-nuchal part is greater in modern skulls, because the brain is bigger and the nuchal muscles less in fossil man. Both the ancient and modern forms are entirely human, and resemble the occipital configuration found in baby apes. In baby anthropoids, as in men, the head is poised upon the body, and the muscles merely fixed for purposes of gentle nodding and turning the head. In men it is so through life, but in the adult anthropoids the head has to become, as it were, an integral part of the trunk in order that the individual may exert its great strength through its huge jaws. The occipital ridge ascends towards the vertex like the temporal, and thus extends the nuchal surface, until a crescentic plateau, continuous with the mastoids, offers a firm attachment for the nuchal muscles.

Dubois throws much stress upon the fact that the occipital ridge (linea nuchæ superior) and linea nuchæ inferior emerge together from the external occipital protuberance (the mesial part of the occipital ridge). These two lines enclose the insertion of the complexus. The complexus has a similar insertion in the gibbon, but I have been unable to find such an insertion in man.[1] It is probably an individual peculiarity. The pit, also, which occurs in the nuchal surface of the Bengawan skull, and marks probably the insertion of the *rectus posticus minor*, is not confined to gibbons, as Dubois has stated, but occurs in many human skulls.

In most of the many lists that give us the differential diagnosis of man, it is stated that he only has a mastoid process. Herein the anthropoids have been wronged; for although the simian mastoid may not have the human form,

[1] Martin (*Globus*, bd. lxvii., No. 14, 1895) states that he has observed a similar arrangement of the nuchal lines in human skulls.

yet it has a much more massive development. Unfortunately, in the Bengawan and Neanderthal skulls the mastoid region is wanting; but the arrangement of the occipital crests in these skulls indicates for us that the heads were poised upon the trunk, so that the mastoids must have been approximately similar to those of modern men. The mastoids of the Spy crania measure from the tip to the meatus roof about 26 m.m.; in the Cynocephalic Australian skulls the measurements vary from 20 to 30 m.m.; while those of modern European skulls are frequently more than 30 m.m. In both human and simian babies the mastoid process is absent; in the first, with years, it grows downwards to give its muscles leverage for gentle nodding and turning movements; in the second, it grows outwards to form the lateral parts of the occipital plateau, and thus enlarge the surface for fixation of the nuchal muscles. This latter also is probably the primitive form, but we cannot say that the fossil human skulls show any approach thereto.

8. CHARACTERISTICS OF THE CRANIAL VAULTS OF HUMAN FOSSIL SKULLS.

The Cynocephalic aspect—the retreating forehead and depressed crown—of the Bengawan, Neanderthal, Spy and some Australian crania is due to the absence of the frontal and parietal flexures of the vault. In most modern crania the frontal is bent so that part of it looks forward and gives a basis to the brow, while the other part enters into the formation of the cranial roof. The parietal is also bent, so that anteriorly it forms part of the roof, posteriorly rather a part of the posterior cranial wall. Why the cranial vault should be flexed abruptly in most modern, and gradually in most fossil, crania is not known, but there can be no doubt that in this respect the fossil crania make a nearer approach to the primitive type and simian form than do modern skulls.

In the Bengawan skull an obtuse ridge runs along the position of the median frontal suture and the anterior part of the sagittal suture. It frequently occurs in human crania

of the cynocephalic type, sometimes in idiots,[1] but has never been observed in anthropoid skulls. Its meaning is quite unknown.

Idiots' skulls[2] not unfrequently manifest these cynocephalic characters, and it has been supposed that the Bengawan skull may have belonged to such an individual. Although idiot skulls manifest a great variety of forms, there has never been one recorded that even approximates the conformation of the Bengawan skull. There is no reason why an idiot may not have such a brain case as that of the Bengawan; only it must be excessively rare, and the chances are enormously against such being found in a fossil state.

9. THE FACIAL PARTS OF FOSSIL SKULLS.

The facial parts of the Bengawan skull are quite wanting. The supra-orbital ridge, which formed the upper boundary of its face, measures from end to end 110 m.m., and the corresponding ridges in the Neanderthal and Spy crania slightly exceed 120 m.m., neither of these measurements differing greatly from those of modern skulls.

Only in Spy cranium No. 1 can the dimensions of the orbit be calculated. Transversely the orbits of that skull measure 40 m.m., and vertically 38 m.m., proportions which are in no way peculiar.

The inter-orbital breadth is, in the Neanderthal skull, 30 m.m.; in Spy cranium No. 1, 30 m.m.; No. 2, 30 m.m.; in Australian skulls, from 22 to 28 m.m.; in negro skulls, frequently over 30 m.m.; in European skulls, frequently over 25 m.m.; in adult gorillas, from 24 to 28 m.m.; in chimpanzees, 22 to 26 m.m.; and in orangs, commonly under 20 m.m. The inter-orbital breadth depends to some extent upon the development of the upper turbinate bones, which in turn depend upon the degree in which the sense

[1] Cunningham and Telford Smith, "The Brain and Cranium of a Microcephalic Idiot," *Trans. Roy. Dub. Soc.*, vol. v., pt. viii., p. 340.

[2] Humphry, "Notes on Nineteen Microcephalic Skulls," *Journ. Anat. and Physiolog.*, Feb., 1895.

of smell is present. In the orang, for instance, the upper turbinate bones are less developed (more rudimentary) than in any of the higher primates, and the inter-orbital space is proportionally narrower. Its extent also depends to some degree upon the size of the ethmoid and lachrymal air-sinuses. Notwithstanding, this space may be used, in the primates at least, as some indication of the acuteness of smell; it may therefore be inferred, from the wide inter-orbital spaces of the fossil men, that this sense was well developed in them.

10. WHAT ARE THE IMPRINTS OF SPEECH UPON THE FACIAL PARTS OF THE SKULL, AND DO HUMAN FOSSIL SKULLS POSSESS THEM?

Of the facial parts of the human skull, specially modified for speech, the prominent ascending nasal processes of the superior maxillary, the short vertical alveolar borders of the jaws, and the presence of a triangular mental eminence, are amongst the chief. Unfortunately, only in Spy cranium No. 1 are the superior maxillaries even fragmentarily represented, but they have every indication of the usual human conformation.

Fortunately, however, the mental space or eminence is completely preserved in two fossil jaws—the Naulette and Spy No. 1. On these two jaws, as on those of all modern men, the mental lines sweep forward above the inferior borders of the jaw until they approach the symphisis menti, when they turn up towards, and meet some distance below, the incisor teeth. They cut off a rough, triangular space with its base at the lower border of the bony chin, and its apex directed towards the teeth. In most modern jaws this space is raised so that it is in advance of the teeth, presenting advantageous points of fixation for the inferior labial muscles. In the fossil jaws the triangular space is not raised; in the Naulette jaw it is flush with the inferior incisors; in the Spy jaw it is behind them. The arrangement of the mental lines being the same in human fossil jaws as in modern ones, one naturally infers that the muscles which arose from them were adapted to similar

purposes, and were therefore subservient for speech. The arrangement of the mental lines in anthropoids is quite different. They turn up in front of the inferior canine teeth, and enclose between them a quadrilateral rough surface corresponding to the triangular mental space of man. In anthropoids this space retreats rapidly downwards and backwards, a feature in which fossil man resembles apes much more than modern man, and shows also, I think, that fossil man was less highly adapted for speech.

Other speech indications are the short wide almost semicircular shape of the jaws, of the palate, and of the dental series; the presence of an incisiform canine, the conformation of the posterior aspect of the mandibular symphysial region, and the prominence of the mylo-hyoid ridge. All these indications are as well marked in the Spy and Naulette as in many Australian jaws. The canines of the Bengawan skull were probably incisiform, as we know from the temporal ridges; and the molar tooth strongly suggests that it possessed a semicircular dental series. The evidences of speech in the Bengawan skull are, however, strictly negative.

11. THE TEETH OF FOSSIL MAN.

Much stress has been put upon the conformation of the teeth, as evidence of the line of descent, by Topinard[1] and Cope.[2] Unfortunately, we know the teeth of fossil men only by more or less worn specimens derived from the Spy, Naulette, Bengawan, Schipka Engis, D'Arcy-sur-Cure and Tilbury finds. The incisors, canines and premolars, although of goodly size, offer no features dissimilar from quite common forms of to-day. On the other hand the

[1] "L'Evolution des Molaires et des Premolaires chez les Primates et en particular chez l'Homme," *L'Anthropologie*, tome iii., 1892, pp. 641-710.

[2] "On the Tribercular Tooth in Human Dentition," *Journal of Morphology*, vol. ii., pp. 1-24; also *American Naturalist*, vol. xx., pp. 941 and 947; also his paper on "The Genealogy of Man," *American Naturalist*, vol. xxvii., p. 316. See also Forsyth Major's paper "On the Teeth of Miocene Squirrels," *Proc. Zool. Soc. Lond.*, 1893.

molar teeth, specimens of which we know from the Spy, Naulette and Bengawan remains, are quite human yet quite peculiar.

The peculiarity of the Spy and Naulette molar series lies not in any singularity in size, but in the complete development of each individual tooth. The Naulette inferior molar series measures antero-posteriorly 31 m.m.; the Spy No. 1, 31 m.m.; the Spy No. 2, 34 m.m.—measurements which are large, but not exceptionally so.[1] The first and second inferior molars of these three individuals are in no way peculiar; the first has five cusps, and the second four, arranged after the usual manner. The third tooth of the lower molar series, however, differs from the vast majority of its modern representatives in being the largest of the series. In the Naulette jaw it measures antero-posteriorly 12·5 m.m.; transversely, 11 m.m.; in Spy No. 1, 11 m.m. × 11 m.m., and in Spy No 2, 11·5 m.m. × 11·5 m.m.

The upper molar series of the fossil men are singular in showing the third molar (wisdom tooth) fully developed. The dimensions of the molar series in the Spy sets are not at all remarkable, measuring in No. 1, 28·5 m.m. antero-posteriorly and 11 m.m. transversely; in No. 2, 33 m.m. × 12 to 13 m.m. The molar series in the Bengawan skull, judging from the size of the third molar, must have been of extraordinary dimensions. The third molar of the Bengawan series measures 11·3 m.m. antero-posteriorly and 15·3 m.m. transversely, against 10 m.m. and 12·5 m.m. —the corresponding dimensions of the third molar of Spy cranium No. 2. Wisdom teeth, which show the greatly subdivided and broken-up arrangement of cusps seen in the Bengawan tooth, never possess, either in anthropoids or men, an antero-posterior diameter more than three-fourths of either the first or second molars. We may infer, therefore, with some degree of certainty, that the Bengawan molar series measured antero-posteriorly at any rate 37

[1] Flower, "The Size of Teeth as a Character of Race," *Journ. Anthrop. Instit.*, vol. xiv., 1885, pp. 182-187.

m.m. A Macrodont Tasmanian skull, in the Museum of the Royal College of Surgeons of England, has a molar series that measures 35 m.m.; the molar series of a Malay skull, in the Museum of Natural History, South Kensington, measures fully 35 m.m., while approximations to these measurements in Macrodont races are not uncommon. But in none of these skulls do the wisdom teeth rival the 15·3 m.m. breadth of the Bengawan tooth, the nearest approach being 14·3 m.m., observed in a South Kensington Malay skull.

The three fangs of the Spy wisdom teeth are not conjoined and fused together as so commonly occurs in modern man, but are separate and distinct as in many Australians and negroid individuals. The two inner fangs of the Bengawan tooth are conjoined.

The four cusps and oblique ridge of the Spy wisdom teeth are fully developed, a development which Cope[1] has seen only once, and that in the tooth of an Australian native. This eminent authority regards the Spy wisdom teeth as characteristic and representative of the early human race, and in the full development of their cusps as an approximation to the common and simian type.

The imperfect development of the upper wisdom teeth is not infrequently stated to be a human attribute; the extent of the imperfection is human; to a greater or less degree it is met with in the wisdom teeth of most chimpanzees, many orangs, and gibbons, but very seldom in the gorilla and siamang. The development of cusps, seen in the Bengawan tooth, is a condition not uncommonly occurring in the wisdom teeth of orangs, chimpanzees, and some negroid individuals. The cusps have become subdivided. The antero-internal cusp (= A.I.), which forms the larger half of this tooth, shows an indistinct separation into three parts. The ridge, which proceeds from this cusp to join with the ridge from the opposite cusp A.E. to form the anterior "rein" of Topinard,[2] is fully developed.

[1] *American Naturalist*, vol. xxvii., p. 316.

[2] *L'Anthropologie*, 1892, p. 641.

The oblique ridge—posterior rein of Topinard—is very partially present, being represented only by that part which springs from the antero-internal cusp. The other three cusps (A.E., P.E. and P.I.), fused together and with the cingulum of the crown, form on the postero-external side of the tooth a crenated border, subdivided into nine minor cusps. This crenated border markedly recalls the multicuspidate buccal margin of the ornithorynchus tooth.

The enamel of the crown is crenated, as one sometimes sees in the wisdom teeth of negroid people. It is the persistence of an embryonic character. Molar teeth of the orang show a somewhat similar enamel-crenation.

12. THE BONES OF THE LIMBS.

Counterparts for the massive and bent Spy and Neanderthal femora can be found in collections of Patagonian skeletons. The Bengawan thigh bone might easily be mistaken for that of a London lady or an Australian woman. The Bengawan femur has every geological claim to antiquity that the calvaria and tooth possess, and stands in a plight exactly parallel to that of the Engis skull—in danger of being rejected because it is of modern form. It seems to me, however, highly probably that the frame of man reached its perfection for pedal progression long before his brain attained its present complex structure. If one conceives this probable or even possible, there is no hindrance to awarding the femur to the Bengawan woman.

All the other bones belonging to the limbs and trunks of fossil men, such fragments as we know of them, support the contention that the human frame was matured before early Quaternary times.

SUMMARY AND CONCLUSION.

Our human geological record stretches as yet back only to an early post-tertiary period.[1] The millions of men that

[1] Dubois uses the ambiguous term Pleistocene—I understand him to refer to an early Quaternary period.

must have lived in these early times are known to us by only four specimens complete enough to permit of their reconstruction. But, taking these as samples of their race, we can say with some assurance that man has not changed much since the Tertiary period of the earth's history closed. The majority of men were distinctly and considerably smaller-brained than the great majority of the men that now people the earth's surface. Their faces, jaws, teeth and muscular ridges were more pronounced. Since Tertiary times the human structural progress has lain in an increase of brain, and a diminution in the masticatory and alimentary systems. In these features we may suppose that early Quaternary man approached the primate ancestors of the race; in these features he certainly comes nearer the present simian type. But, for the purpose of giving us a clue to the human line of descent, the fossil remains at present known assist us not one single jot. Their configuration is quite conformable to the theory of a common descent; they bear out the truth of that theory. They also show us that man since the Tertiary period has changed structurally very little. There is nothing remarkable in this, for allied primate forms (*Paleopithecus sivalenses*[1] and *Dryopithecus*[2]) demonstrate to us that, since the Miocene period, the anthropoid type has changed but slightly. We need not then be surprised at being obliged to seek deep within the Tertiary formations the evidences of human descent.

ARTHUR KEITH.

[1] Lydekker, "Further Notices of Siwalik Mammalia," *Records of the Geological Survey of India*, vol. xii., 1879, p. 33.

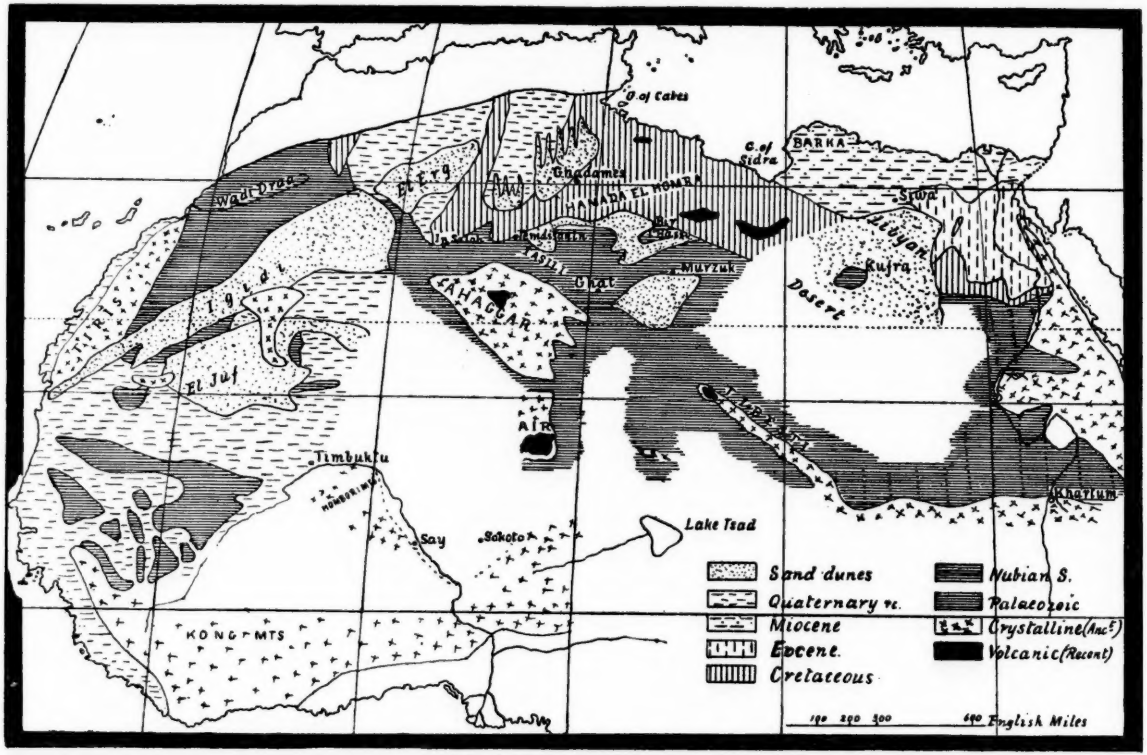
[2] Gaudry, *Mem. Soc. Geol. France*, vol. i.

THE GEOLOGY OF THE SAHARA.

IN the eyes of a geologist, Northern Africa, with all its political complications, falls into two, and only two, great divisions. They are of very unequal extent, and the boundary between them lies along the southern flanks of the Atlas Mountains. In the northern division, in Tunis, Algeria, and Morocco, the rocks have been thrown into folds which run somewhat north of east; and these folds have given rise to mountain chains approximately parallel to the Sierras of Spain. This part of Africa, indeed, as even so ancient a writer as Sallust has remarked, is physically a part of Europe. South of the Atlas, on the other hand, even the Devonian and Carboniferous beds are nearly horizontal, and they form broad plateaux instead of narrow mountain chains. It is this division, the Sahara, with which the present article is concerned.

Sahara is a word of doubtful origin, and in its application it is somewhat vague. In its widest sense it includes the whole of that portion of Africa which extends from the Atlas southwards to the fertile districts of the Soudan; and from the Atlantic eastwards to the borders of the Red Sea. Even the shores of the Mediterranean, from the Gulf of Cabes to the Suez Canal, belong to it; and Egypt and the Nubian Desert lie within its limits. But to confine the article within reasonable bounds, the valley of the Nile and the regions to the east must be left for future consideration.

In its physical features the Sahara of Northern Africa is very different from the Sahara of our older text-books. It is not the broad, low-lying waste of sand which they depict; but the greater part is occupied by a succession of elevated rocky plateaux, and the sandy deserts form a comparatively small part of the whole. The largest of the sandy wastes is the Libyan Desert, between Fezzan and the Nile; while in the west the most extensive are those of Igidi and El Juf.



GEOLOGICAL SKETCH OF THE SAHARA.

The Pliocene deposits are included with the Quaternary in this map.

In the centre of the region rise several mountain masses of considerable altitude. The most important is the Tarso range in Tibesti, the culminating peak of which is estimated by Nachtigal to attain a height of about 7900 feet. Another great mountain mass is the Ahaggar, in the country of the Tuareg. Both of these are supposed to consist of Archæan rocks : the sedimentary deposits form plateaux rather than mountains.

Even the sandy wastes themselves lie at a considerable elevation ; and the only parts of Northern Africa which are sunk beneath the level of the sea are the Tunisian Shotts, west of the Gulf of Cabes ; and perhaps a strip of country between the Gulf of Sidra and the Oasis of Siwa, or Jupiter Ammon. The Shotts have been carefully surveyed by the French Government (1) ; but the elevation of the oases west of Siwa has been determined only by barometrical observations, and the results of two expeditions differ by more than 100 metres.

So greatly do the plateaux exceed the lower lying districts in extent, and so considerable is the elevation even of the deserts, that Chavanne estimates the average height of the Sahara at 460 m. (2) above the sea-level, and according to him the region is constituted as follows (3, p. 789) :—

Hamadas and Serirs,[1] 3,600,000 sq. kilos ; steppes, 1,500,000 sq. kilos.
Rocks and mountains, 2,000,000 „ sand, 350,000 „
Oases and cultivated ground, 200,000 sq. kilos.

For fuller information on the physical features of the Sahara, I cannot do better than refer to the admirable description in Reclus' *Géographie Universelle* (3), and to the monograph of H. Schirmer (4).

Although many travellers have penetrated into the difficult and dangerous regions of the Sahara, few of them have had any pretensions to a knowledge of geology.

[1] The Hamadas and Serirs are stony plateaux destitute of vegetation and almost of soil.

The earlier explorers, such as Lyon (5), and Denham and Clapperton (6), lived before the days of modern geology. It is true that Lyon's specimens were examined by Buckland (5, pp. 361-369), and Denham's by Konig (6, pp. 247-261); but the specimens were too few and the state of the science too imperfect to allow of any but erroneous conclusions. In more recent years, misfortune has attended the footsteps of two at least of the few who have been qualified to make geological observations. The French geologist, Roche, perished in the massacre of the ill-fated second expedition under Flatters; and Overweg, the companion of Richardson and Barth, fell a victim to the climate of the shores of Lake Tsad.

We are compelled then to rely, to a considerable extent, on scattered observations made by travellers who devoted themselves chiefly to other matters; and if it were not that the structure of the region is singularly simple, the geology of the Sahara would be almost unknown. But the imperfect notes of these explorers serve to fill in the gaps left between the fuller observations of more skilled geologists; and it is possible, as Rolland and others have shown, to form a picture of the geological structure of the whole region. No doubt such a sketch as our present materials allow, will be faulty, and undoubtedly it must be incomplete; but it cannot be entirely devoid of interest, and if its imperfections be borne in mind, it may not be without its use.

Pomel (7) was the first to attempt a general description of the geology of the Sahara; and although our knowledge is wider now, his account is still of value. More recently Zittel (8) and Suess (9) have endeavoured to collect and harmonise the geological notes of travellers in these regions; and within the last few years Rolland (10, 11) has applied himself to the same task.

The explorers to whom these writers look for the principal part of their facts are Lenz (12) in the Western Sahara, Roche (13, 14) and Rolland (15) in the Algerian Sahara, Overweg (16, 17) in Tripoli and Fezzan, and Zittel (8) in the Libyan Desert. The accounts of these

regions are tolerably complete ; but in the central parts of the Sahara we have little besides the notes of Barth (18) and Rohlfs (19), who were not geologists. It is to be regretted that so careful an observer as Nachtigal (20) should have told us so little of the character of the rocks over which he passed.

With regard to maps the Sahara is highly favoured, for so inhospitable a country. The sketches of Suess and Rolland are accompanied by geological maps, and Zittel is responsible for the map of Africa in Berghaus' Geological Atlas (21). Rolland's map, with some slight alterations and improvements, is reproduced by Schirmer (4, p. 9).

All these general maps are based mainly upon Lenz' geological map of West Africa (22), Rolland's of the Algerian Sahara (15), and Zittel's of the Libyan Desert (8).

Speaking broadly, the Sahara is geologically the southern half of an enormous basin. The outer rim, which is not perfect, is formed by granite, gneiss, and other crystalline rocks, presumed to be of Archæan age. Such rocks occur along the west coast, south of the Wadi Draa, and throughout the Tiris country. In Senegambia they are replaced by slates and quartzites, doubtfully referred to the Silurian. But gneiss reappears in the Kong Mountains, and there is reason to believe that Archæan rocks extend nearly continuously across the Soudan as far as Khartum. Here again, as in the west, the rim is broken by a strip of later rocks ; but granite and gneiss reappear further north, and form the eastern border of the continent.

Within this rim there is a vast area of Palæozoic rocks, while the centre of the basin is occupied by Cretaceous and Tertiary deposits. Jurassic beds are unknown except in the extreme north, on the borders of Tunis (23); and of the Trias there is probably no trace.[1]

Granitic and gneissic rocks.—On Lenz' map of West Africa, a broad belt of Devonian and Carboniferous rocks

[1] Berghaus' map shows Trias and Dyas at various points on Barth's route from Kuka to Timbuktu, and a large area in Kordofan. Of the first the evidence is extremely unsatisfactory ; the second will be discussed in a future article.

is marked in the north-western part of the Sahara. The whole of the Igidi Desert and most of the land between this and the Atlas is included in the belt. But the country of Tiris, which lies north of Cape Blanco, is coloured as a wedge of Quaternary deposits between the older rocks and the sea. Vincent, however, long ago described Tiris as a granitic plateau (24, p. 23), and more recently Quiroga has shown that the greater part of the district is occupied by granitic and gneissic rocks (25). Some of these he refers to the Archæan, while others (including an elæolite syenite) he believes to be eruptive. There is a narrow band which he considers to be of Palæozoic age.

Douls, too, describes granite on both sides of the Wadi Chebika (south of the Wadi Draa) (26, p. 456); and it is probable that granitic rocks form a belt along the west coast, separated from the sea by a narrow band of Pliocene and recent deposits.

This belt of crystalline rocks, however, does not appear to extend far to the south. West of Shinghit, Panet (27, pp. 103, 104) describes the occurrence of slate, agglomerate and sandstone, together with what he believed to be basalt. Lenz has coloured these as Silurian. In Senegambia, too, which Lenz himself has traversed, his map shows the whole region to be made of slate and quartzite, with laterite in the valleys (22). It is not till we reach the Kong Mountains that we again come upon an extensive area of gneissic rocks.

The gneiss of these mountains probably extends into the bend of the Niger nearly to Timbuktu; for Barth, on his journey from Say to that town, noted granite at several points (see map in 18, vol. iv.). The most remarkable, however, of the rocks which he observed, were in the Hombori Mountains. In his sketch (18, iv., p. 336) these hills appear like lofty towers resting upon conical mounds of detritus. It is difficult to believe that gneiss or granite could weather into these forms, and they are more suggestive of columnar lavas. Barth himself does not state the character of the rock, although on his map he records a granitic peak close by. But whatever the Hombori hills

may be, the number of points at which granite occurs justifies us in concluding that a large part of the region enclosed in the great bend of the Niger is composed of granite or gneiss.

It does not appear, however, that these rocks extend much farther to the north. It is true that Barth notes granitic boulders in the course of the Niger some 150 miles east of Timbuktu; but near the point where the river bends from east to south, stratified rocks occur on the north side of the river, and south of Gogo there are steep sandstone cliffs. At Say itself sandstone also occurs.

East of the Niger, between Say and Sokoto, and again nearly as far as Katsena, there are no records of rock, and the country is for the most part a plain. But a little west of Katsena, Barth again mentions granitic rock; and granite also occurs at intervals as far as Mashena.

We have now traced the granitic rim of the Sahara basin from the Tiris country to the plains of Lake Tsad, where it is lost under recent deposits. But there are several masses of granite which appear to be separated from the main belt, and which rise up in the midst of the sedimentary deposits within the basin. Lenz records granite in El Eglab on the southern border of the Igidi Desert (12, vol. ii., p. 60); and according to Barth, a considerable part of the Aïr country is made of granite. In Aïr it is associated with flows of basalt, and both on the north and the south it is overlaid by the sandstone which occupies such wide areas in the Central Sahara (18, vol. i.).

But a much more extensive Archæan mass than either of these, is that which forms the Ahaggar. Both Barth and von Bary passed to the east of these mountains on their way from Ghat to Aïr; and both of them found the country, from the Wadi Egeri southwards, to consist mainly of granite (18, vol. i., map; 29, 12th Jan., 1877). Here and there the granite is overlaid by plateaux of sandstone, which seem to be tongues projecting west from the more extensive plateau crossed by Nachtigal and Rohlfs on their way to Kuka.

Into the centre of the Ahaggar no European traveller

has yet penetrated; but it is probable that the granite which Barth and von Bary crossed, is simply the eastern part of a mass of crystalline rock of which the Ahaggar is the centre. It is true that Ismail-Boû-Derba is said to have found pebbles of lava in the Wadi Igharghar, and these pebbles appeared to have come from Ahaggar (30, p. 54). If this be so, there are probably lava-flows in these mountains just as in the hilly granitic region of Aïr.

Barth's and von Bary's observations, in conjunction with those of Rohlfs, give us the eastern boundary of the Ahaggar massif; and the northern limit is determined by the discovery of Devonian fossils in the Tasili plateau. But the southern boundary is less certain. Rolland assumes that the Tasili-wan-Ahaggar, south of the great Ahaggar, is a Palæozoic plateau. This cannot be said to be certain; but it seems likely that the granitic rocks do not extend far to the south of the mountain mass itself.

East of Ahaggar and Aïr there is sandstone, but it is uncertain how far this extends to the south. According to Rohlfs, granite occurs in the Geissiger Mountains (19, vol. i., p. 272); but sandstone and limestone still predominate. It is not till we proceed to the east that we meet with any more granitic rocks. At the north-west end of the Tibesti Mountains, Nachtigal has noticed the presence of granite (20); and from this and the character of the hills, Suess infers that the whole range is Archæan.[1] If this be correct, it probably forms only a narrow strip, for sandstone hills occur on the south side of the range in the district of Borku.

This narrow strip is probably connected on the east with the extensive mass of Archæan rocks in Kordofan and Sennaar;[2] but the intermediate country requires examination. Near Khartum these rocks are succeeded by the Nubian sandstone; but farther north there is another large

[1] From Nachtigal's description I cannot but think that the main mass of this range is Palæozoic rather than Archæan (20, vol. i., pp. 389-391).

[2] I have for the present followed Suess and Rolland in including the Kordofan and Sennaar rocks in the Archæan. Zittel, in Berghaus' map, has coloured the region as Trias and Dyas, with Archæan masses rising through it.

crystalline mass, which occupies most of the Nubian desert and sends a long and narrow tongue along the shores of the Red Sea as far as the Gulf of Suez. This great Archæan mass forms the bed of the Nile for a considerable distance, but it nowhere extends far to the west of that river.

Palæozoic.—The gneiss of the Kong Mountains is succeeded to the north, in Senegambia, by the extensive area of slates and quartzites which Lenz refers with doubt to the Silurian. He found the same beds at intervals between the Igidi Desert and Timbuktu; and it would appear therefore that these rocks form a belt stretching from Senegambia towards the north-east (22).

They are succeeded on the north-west by a second broad belt of later beds, which Lenz found to extend from the Wadi Draa to the granites of El Eglab. These consist of limestones and sandstones; and at Jerf-el-bir and other places south of Tenduf, he obtained crinoids, brachiopods, and other fossils in abundance. His collections have been examined by Stache, and include numerous species of *Productus*. *Spirifer*, *Chonetes*, *Streptorhynchus*, and other brachiopods also occur; *Cyathophyllum* and other corals; crinoids, including *Poteriocrinus*; and a variety of polyzoa and other forms (31). The general character of the fossils is undoubtedly Carboniferous, but a few of the specimens show Devonian affinities.

The northern boundary of the Palæozoic rocks is drawn by Lenz along the foot of the Atlas as far as the desert El Erg. On the other side of this the Cretaceous beds of the Mzab, El Goleah, and In Salah form a plateau with an escarpment running from north to south. The boundary of the Palæozoic rocks must therefore turn to the south under the sands of the Erg, and it probably lies along the foot of the plateau.

At In Salah the escarpment turns towards the east. The plateau is formed of Cretaceous beds; but the rocks on which they rest are Palæozoic,—for Ismail-Boû-Derba found Devonian beds at the foot of the plateau near Temassanin (30, p. 63). East of Temassanin the boundary

of the Palæozoic rocks runs along the escarpment of the great Hamada el Homra. At Bir el Hassi Overweg found that the Cretaceous beds of the top of the Hamada rest upon sandstone and marl, in which he discovered the Devonian fossils *Spirifer Bouchardi*, *Terebratula* [*Rhynchonella*] *Daleidensis*, *T.* [*R.*] *longinqua* (17).

Continuing the line between the Palæozoic and Cretaceous along the escarpment of the Hamada, we find that it leads us to the Libyan Desert, where nothing is known of the rocks until we reach the oasis of Kufra.

Throughout the whole of the area from the Cretaceous escarpment southwards to the gneissic series, the Palæozoic beds are nearly horizontal, and they consist for the most part of sandstone resting upon marl or marly slate. This is well seen in the Akakus range, east of Ghat, of which a sketch is given by Barth. Fossils have been found in the sandstone and marl at several places besides those already noticed. In the Tasili plateau Roche discovered a trilobite allied to *Proetus Cuvieri*, a tail of *Calymene* (?), *Strophomena quadrangularis*, *Atrypa prisca*, *A. reticularis*, *Orthis*, *Spirifer*, and *Rhynchonella ;* and he concludes that these beds are of Devonian age (13). At the northern end of the Akakus range Duveyrier found fossils which were referred by De Verneuil to *Spirifer* (near to *Sp. ostiolatus* and *Sp. subcuspidatus*), and *Chonetes crenulata.* Here again a Devonian age is indicated (30, p. 62).

East of the Libyan Desert, which causes a serious break in the continuity of our map, it is the so-called Nubian sandstone which rests upon the crystalline rocks. It occupies a large space between the Cretaceous of the Dakhla Oasis and the Archæan rocks of Upper Egypt, and it is found also in the Oasis of Kufra (32, p. 330). The geological position of this sandstone has been much discussed, for till recently no fossils had been found in it except silicified wood. From the fact that the Upper Cretaceous of the Libyan Desert is quite conformable upon it, Zittel concluded that it must probably be of Lower Cretaceous age. But the discovery of Carboniferous

fossils by Schweinfurth in the Wadi Araba[1] (33), has led most subsequent writers to refer a part of the series to the Palæozoic. Rolland indeed has gone so far as to include the whole of the Nubian sandstone with the Palæozoic upon his map; but this is due no doubt simply to the impossibility, in the present state of our knowledge, of drawing a line between the Upper and Lower divisions.

Cretaceous.—Turning now to the Cretaceous deposits, we find that in the Algerian Sahara they form the plateaux of the Mzab and Tedmaid (near In Salah); and in Tripoli the Hamada el Homra. The southern and western boundaries have already been traced, and the Cretaceous rocks, except where covered by later deposits, extend from these boundaries to the Atlas and Mediterranean. Between the Mzab and the Hamada el Homra lies a broad area of Quaternary deposits, through the middle of which runs the depression called the Wadi Igharghar—a depression which figures very prominently in certain accounts of North Africa, but which is not everywhere very clearly defined.

Rolland (15) finds that the Cretaceous plateau of the Algerian Sahara rises in two steps or terraces; the lower terrace being formed of Middle Cretaceous and the upper terrace of Upper Cretaceous beds. Each consists of a limestone, resting upon a series of gypseous marls; and the lower stage is often very fossiliferous. Among the fossils are *Ostrea flabellata*, *Plicatula auressensis*, both of them essentially Cenomanian forms; and a variety of other species, nearly all of which are common in the Cenomanian of the Atlas.

In the Algerian Sahara no fossils have been found in the upper stage, but in Tripoli they are fairly abundant.

On the north edge of the plateau that lies south of the town of Tripoli, Overweg (16, 17) discovered *Rudistes*, *Exogyra sinuata*, and *Ex. conica*. These are Cenomanian, and the beds in which they occur clearly correspond with

[1] This is the Wadi Araba which opens into the Gulf of Suez, about 29° N. Lat., *not* the Wadi Araba of Syria.

the lower of Rolland's terraces. On the top of the plateau the same explorer obtained *Inoceramus impressus*, *Cardita*, *Arca*, *Exogyra Overwegi*, and *Ostrea larva*; the first and last of which are Senonian forms, while *Ex. Overwegi* is almost peculiar to the Sahara.

Other travellers also have found Senonian fossils upon this plateau. The collections made by Vatonne on his journey to Ghadames have been examined by Coquand (15, p. 545). They include *Ostrea vesicularis*, *O. larva*, *O. ostracina*, *O. Overwegi*, and several other Senonian forms, together with a few Cenomanian species. Rohlfs also, on the way to Ghadames, found *Ostrea armata*, *O. larva*, *Exogyra Overwegi*, and *Ex. Matheroniana* (34); while south of that town, Duveyrier discovered the Cenomanian form, *Exogyra columba*, near the southern escarpment of the plateau (30, pp. 49, 50).

It is tolerably clear then that the Tripoli plateau, the Hamada el Homra, is formed of Senonian beds, resting upon Cenomanian, and perhaps Turonian; and this agrees with Rolland's observations in the Algerian Sahara.

Farther east, the "Black Mountains" (Jebel el Soda and Jebel Haruj) rise up amidst the Cretaceous rocks. They have been the subject of much discussion; but are probably in part volcanic, and will be described in speaking of the eruptive rocks.

On the eastern side of the Libyan Desert the Cretaceous and later beds have been very fully described by Zittel (8), who accompanied one of Rohlfs' numerous expeditions. But I shall confine myself here to a very brief and general account of the character and distribution of these deposits; the details will come more fittingly in a description of Egypt and the Valley of the Nile.

The Nubian sandstone of Upper Egypt is succeeded conformably by a series of Cretaceous limestones and marls, which occupy the floors of the Kharga, Dakhla, and Farafra Oases, and stretch away westwards beneath the sands of the desert. The whole series belongs to the Upper Cretaceous; and the lower beds, which contain *Exogyra Overwegi* in abundance, correspond with the upper

beds of the Hamada el Homra. Unless, then, the Nubian sandstone is in part Cretaceous, the Cenomanian of the Western Sahara is absent in the east, and has been overlapped by the higher beds. That the Cretaceous beds of Egypt do overlap the beds below, is shown by the fact that east of the Nile they rest for many miles directly upon the crystalline rocks, whereas in the Libyan Desert they lie conformably upon the Nubian sandstone.

Tertiary.—It is only in the eastern part of the Sahara, east of the Libyan Desert, that Eocene beds are developed. They cover a wide area north of the Cretaceous belt of the oases, and they consist chiefly of limestones. West of the Nile they lie upon the Cretaceous beds; but east of the ruins of Thebes they rest for a short distance upon the crystalline rocks.

Towards the north and west the Eocene deposits pass under Miocene beds. In the Oasis of Siwa these consist of limestones, sandstones, and clays; and the lower beds are marine, while the upper are of freshwater origin. The freshwater beds are probably the equivalents of the Jebel Ahmar sandstone and the remarkable fossil forests of Cairo (35).

The Miocene beds extend along the southern shore of the Mediterranean, from the delta of the Nile westwards as far, no doubt, as the Gulf of Sidra. They occupy the Oasis of Siwa, and they probably form the whole of the Barka plateau (8, p. 131). They seem, like the other deposits of this region, to overlap the beds below; and in Tripoli they rest directly upon the Cretaceous.

The Pliocene of the Sahara is insignificant in extent, and structurally of little importance. Lenz, in his map of West Africa, has coloured a narrow strip of Cretaceous rocks along the West Coast from Morocco to Cape Blanco; and most subsequent cartographers have accepted his authority. But it appears from the researches of Quiroga at Rio d' Oro that the coast is formed, not of Cretaceous, but of Pliocene deposits. Limestones, sandstones, and marls occur, in which Quiroga has found a very recent fauna, including many living species (25).

Pliocene beds are also found in Egypt, but these need not be considered here.

Quaternary.—Quaternary deposits cover wide areas in the Sahara, and were at one time supposed to be of marine origin. It was even held that the great sand dunes of the deserts must have been formed under the sea; but at this date it is scarcely necessary to discuss such a view. There are many other points of interest in connection with the dunes; but space does not permit me to touch upon them. and I can only refer to the work of Walther on denudation in the deserts (36).

The advocates for a Quaternary Sahara sea argued chiefly from the discovery of marine shells at several points in the middle of the Sahara. But Tournouër has shown that to call in the aid of a great ocean in order to explain the presence of one or two shells is a needless expenditure of energy (37). Indeed it would be difficult for the ocean to have deposited them without leaving more extended evidence of its existence; and in some cases, at least, the shells seem to have been brought by man, like the money cowries in use at the present day.

Eruptive rocks.—It is probable, to say the least, that much of the granitic rock observed by travellers is of eruptive origin, and some of it may well belong to a much later period than the Archæan. But the evidence is generally incomplete.

In the Tiris country, Quiroga (25) describes granite and elæolite syenite, which he believes to be eruptive and distinct from the Archæan. Eruptive rocks of basic character also occur in this region. Both Douls (26) in the north, and Panet (27) in the south, speak of basalts; and Quiroga also has described the occurrence of diabase and melaphyre.

Von Bary, in the diary of his journey from Ghat to Aïr, notices basalt in connection with the granite; and according to him, Tegindshir in Aïr is an extinct volcano (29, p. 362, etc.). Barth, also, in his account of the same region, describes Teléshera as consisting of sandstone, capped by trachyte; and further south he records a terrace of basalt (18, vol. i., p. 501).

Again, at the north-west end of the Tarso range, Nachtigal describes a well-formed crater; and this clearly points to a recent period of vulcanicity (20, vol. i., pp. 389-391).

In none of these cases, however, is there any really satisfactory evidence of the age of the rocks; and it is only among the more recent deposits, the Cretaceous and Tertiary, that we are able to fix a definite limit for the date of the eruptions. Near the northern border of the Tripoli plateau several cones of volcanic rock rise through the Cretaceous beds; and these must clearly be of late Cretaceous, or more likely, of Tertiary age. They consist chiefly of phonolite, and to a certain extent, of olivine basalt (16).

But the most extensive volcanic masses in this area are probably the Jebel-el-Soda and the Jebel Haruj, or the "Black Mountains". Hornemann long ago mentioned the presence of basalt in these mountains; but there can be little doubt that he has sometimes been misled by the peculiar black weathering of the surface which is so characteristic of the Sahara—a mode of weathering which gives a very deceptive volcanic look to the sandstones and other rocks which cover so wide an area. In this case, however, Hornemann was probably correct, for Duveyrier brought home specimens which were determined by Descloiseaux to be amygdaloidal basalt (30, p. 77).

It is probable, however, that the eruptive rocks do not form the whole of this mountain mass. Beurmann states that he has nowhere found any traces of basalt, and he can scarcely believe in its presence (38). Vogel, too, describes the range as consisting of limestone and sandstone (39); and Rohlfs, who accepts Duveyrier's view, also speaks of the presence of sedimentary rocks (19, p. 125). We can only conclude, then, that these mountains form a continuation of the Cretaceous plateau, penetrated here and there by eruptive rocks of later date.

Volcanic rocks are also supposed to occur in the Ahaggar Mountains (30, p. 54), and on the Tasili plateau.

Lastly, in the Egyptian area, basalt occurs in the

Baharia Oasis (8), and near Abu-Zabel on the Ismailia Canal (40). In both cases it is of Tertiary age.

On the whole, then, volcanic activity has never been rife in the Sahara, although a little farther south, in Abyssinia and the Somali country, there are vast areas of lava comparable in extent with the Deccan Trap of India.

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PHILIP LAKE.

RECENT VALUES OF THE MAGNETIC ELEMENTS AT THE PRINCIPAL MAGNETIC OBSERVATORIES OF THE WORLD.

[Continued through the courtesy of the Kew committee as in July, 1894.]

IN the case of a few of the observatories data have been supplied by the courtesy of the directors more recent than those in their latest publications, but in the great majority of instances recourse has been had to the publications themselves. In one or two cases the values given last year have had to be repeated. The observatories are arranged according to their latitude. The longitude is in all cases referred to Greenwich. In some few cases where the geographical position had to be extracted from a map, and in others where conflicting statements existed, there may not unlikely be appreciable error.

The data in the table are deduced from hourly readings of the magnetic curves in the case of Pawlowsk, Katharinenburg, Copenhagen (Declination and Horizontal Force), Hamburg (Declination), Wilhelmshaven (Declination and Horizontal Force), Irkutsk, Potsdam, Utrecht (Declination), Kew, Greenwich, Uccle (Declination), Falmouth (Declination and Horizontal Force), Parc Saint Maur, Vienna, Pola, Perpignan, Tiflis, Nice (Declination), Washington, Zi-ka-wei, Manila, Batavia, and Mauritius (?).

In the case of Madrid (Declination), Prague (Declination), O'Gyalla (Declination and Horizontal Force), Coimbra (Declination), Lisbon (Declination), and Kasan (Declination and Horizontal Force), the diurnal inequality has been at least partly, in some cases probably with great exactness, allowed for by taking readings from curves or absolute instruments at two or more different hours.

For the explanation of the apparent rise in Vertical Force at Kew since 1893, see "The Report of the Incorporated Kew Committee," *Roy. Soc. Proc.*, 1895. The first results of Greenwich Inclination and Vertical Force are deduced from readings with 3 inch dip needles only, the second from

3, 6, and 9 inch needles. A correction of $-5'{\cdot}1$ has been applied to the mean published value of the Declination at Potsdam; see *Ergebnisse der Magnetischen Beobachtungen in Potsdam in 1890-91*, pp. 79. The values of Horizontal Force and Vertical Force at Batavia, published in last year's tables, should be altered to ·36754 and ·20345 respectively; see the preface to *Observations at Batavia*, vol. xvi. Batavia, 1894.

Place.	Latitude.	Longitude.	Year.	Declination.
Pawlowsk	59° 41′ N.	30° 29′ E.	1893	0° 4′·4 E.
Katharinenburg	56° 49′ N.	60° 38′ E.	1893	9° 34′·6 E.
Kasan	55° 47′ N.	49° 8′ E.	1892	7° 30′·8 W.
Copenhagen	55° 41′ N.	12° 34′ E.	1893	10° 47′·7 W.
Stonyhurst	53° 51′ N.	2° 28′ W.	1894	18° 44′·1 W.
Hamburg	53° 34′ N.	10° 3′ E.	1893	11° 54′·3 W.
Wilhelmshaven	53° 32′ N.	8° 9′ E.	1892	13° 10′·1 W.
Potsdam	52° 22′·9 N.	13° 4′ E.	1891	10° 42′·2 W.
Irkutsk	52° 16′ N.	104° 16′ E.	1893	2° 9′·4 E.
Utrecht	52° 5′ N.	5° 11′ E.	1893	14° 28′·5 W.
Kew	51° 28′ N.	0° 19′ W.	1894	17° 23′·0 W.
Greenwich	51° 28′ N.	0° 0′	1894	17° 4′·6 W.
Uccle (Brussels)	50° 48′ N.	4° 20′ E.	1893	14° 48′·7 W.
Falmouth	50° 9′ N.	5° 5′ W.	1893	19° 6′·4 W.
Prague	50° 5′ N.	14° 25′ E.	1893	9° 42′·3 W.
Parc St. Maur (Paris)	48° 49′ N.	2° 29′ E.	1892	15° 26′·9 W.
Vienna	48° 15′ N.	16° 21′ E.	1893	8° 49′·7 W.
O'Gyalla (near Buda Pesth)	—	—	1894	7° 58′·2 W.
Pola (on Adriatic)	44° 52′ N.	13° 50′ E.	1894	9° 52′·6 W.
Nice	43° 43′ N.	7° 16′ E.	1893	12° 32′·7 W.
Toronto	43° 39′·6 N.	79° 30′ W.	1893	4° 36′·4 W.
Perpignan	42° 42′ N.	2° 53′ E.	1892	14° 16′·0 W.
Rome	41° 54′ N.	12° 27′ E.	1891	10° 45′ W.
Tiflis	41° 43′ N.	44° 48′ E.	1892	1° 33′·6 E.
Madrid	40° 25′ N.	3° 40′ W.	1893	16° 14′·2 W.
Coimbra	40° 12′ N.	8° 25′ W.	1893	17° 51′·7 W.
Washington	38° 53′ N.	77° 0′ W.	1891	4° 9′·7 W.
Lisbon	38° 43′ N.	9° 9′ W.	1893	17° 49′·4 W.
Zi-ka-wei	31° 12′ N.	121° 26′ E.	1892	2° 14′·4 W.
Hong Kong	22° 18′ N.	114° 10′ E.	1893	0° 31′·2 E.
Colaba	18° 54′ N.	72° 49′ E.	1893	0° 40′·3 E.
Manila	14° 35′ N.	127° 11′ E.	1892	0° 50′·1 E.
Batavia	6° 11′ S.	106° 49′ E.	1893	1° 30′·6 E.
Mauritius	20° 6′ S.	57° 33′ E.	1892	10° 5′·1 W.
Melbourne	37° 50′ S.	144° 58′ E.	1893	8° 9′·6 E.

Place.	Year.	Inclination.	Horizontal Force. C. G. S. Units.	Vertical Force. C. G. S. Units.
Pawlowsk	1893	70° 43′·9 N.	·16446	·47046
Katharinenburg	1893	70° 39′·1 N.	·17801	·50694
Kasan	1892	68° 36′·2 N.	·18551	·47345
Copenhagen	1893	68° 51′ N.	·17358	·44868
Stonyhurst	1894	69° 2′·2 N.	·17133	·44719
Hamburg	1893	67° 45′·4 N.	·18003	·44022
Wilhelmshaven	1892	67° 57′·3 N.	·17917	·44245
Potsdam	1891	66° 44′·1 N.	·18635	·43342
Irkutsk	1893	70° 9′·4 N.	·20117	·55744
Utrecht	1893	67° 12′·2 N.	·18397	·43772
Kew	1894	67° 26′·0 N.	·18251	·43914
Greenwich	1894	67° 18′·7 N. 67° 17′·3 N.	·18287	·43742 ·43691
Uccle	1893	66° 28′·4 N.	·1877	·4311
Falmouth	1893	67° 5′·3 N.	·18455	·43665
Prague	1893	—	·19789	—
Parc St. Maur	1892	65° 9′·2 N.	·19584	·42294
Vienna	1893	63° 13′·7 N.	·20724	·41077
O'Gyalla	1894	—	·21054	—
Pola	1894	60° 37′·3 N.	·22004	·39086
Nice	1893	60° 26′·4 N.	·22198	·39139
Toronto	1893	—	·16630	—
Perpignan	1892	60° 14′·3 N.	·22264	·38934
Rome	1891	58° 4′·6 N.	·2324	·3730
Tiflis	1892	55° 46′·1 N.	·25686	·37751
Madrid	1893	—	—	—
Coimbra	1893	59° 50′·5 N.	·22518	·38752
Washington	1891	71° 5′·1 N.	·19855	·57940
Lisbon	1893	58° 24′·6 N.	·23270	·37840
Zi-ka-wei	1892	46° 7′·0 N.	·32500	·33792
Hong Kong	1893	31° 56′·8 N.	·36435	·22720
Colaba	1893	20° 35′·1 N.	·37437	·14060
Manila	1892	17° 7′·2 N.	·37643	·11594
Batavia	1893	29° 6′·2 S.	·36741	·20451
Mauritius	1892	54° 48′·2 S.	·24003	·34030
Melbourne	1893	67° 17′·0 S.	·23432	·55969

CHARLES CHREE.

A TYPE OF PALÆOZOIC PLANTS.

IN the Hof-Museum of Vienna there are some well-executed and striking wall paintings of Upper Carboniferous scenery, designed by Hoffmann, under the direction of the late Dr. Stur. Arborescent Lepidodendrons, Sigillarias and Calamites occupy the most prominent position; and with the large-leaved *Cordaites* these plants probably formed the most conspicuous types in the Upper Palæozoic forests. Some of the Calamites are represented with tall ribbed stems, bearing lateral branches and cones of various forms; among the calamitean foliage we notice the well-known wedge-shaped leaves for which Brongniart, in 1822, instituted the genus *Sphenophyllum*.

Restorations of this kind have been attempted by numerous artists, inspired by widely different views as to the actual appearance of the commonest Coal-Measure plants. In many respects the Viennese pictures may no doubt be regarded as a closer approximation to the truth than most of the earlier attempts, but in certain particulars they are still far from photographic accuracy. It is quite clear, from what we know of the structure of calamitean plants, that in most forms the external surface of the stem did not show any signs of the ridges, grooves or nodal constrictions which form such characteristic features of the common medullary casts. It may be that in some species the stem was slightly ribbed, as suggested by Weiss[1] and other writers,[2] but in the great majority of calamitean plants the surface was no doubt smooth. According to Stur, *Asterophyllites* and *Annularia*, with their univeined leaves, should be regarded as the homomorphous branches of *Calamites*, while *Sphenophyllum*, with broader leaves usually traversed by several veins, represents a heteromorphous form of calamitean branch. Stur's views as to the con-

[1] Weiss (2).

[2] Kidston, *Trans. Geol. Soc. Glasgow*, vol. viii., p. 52.

nection between *Calamites* and *Sphenophyllum* have not been supported by recent work, and we are now in possession of abundant evidence in favour of the autonomous nature of the latter genus.[1] The Calamite must have had somewhat the appearance of a magnified arborescent Equisetum, its underground rhizome growing more or less horizontally, or erect, in the sand or mud, giving off from the nodes numerous adventitious roots, and woody aerial shoots, which grew to a considerable height, and attained a girth of several feet. From the nodes were developed lateral branches, differing in number and disposition in the several forms of the genus, and whorls of numerous univeined leaves replaced the nodal leaf-sheaths of the recent horse-tails. The long and narrow cones were borne on slender pedicels, and in the same cone there were occasionally macrospores and microspores, but probably more commonly the spores were all of one size. As regards the development of the plant, we may reasonably suppose that it was formed as the result of fertilisation of an egg-cell developed on a sexual prothallus, and possibly from the oospore there would be first formed a rhizome structure from which the calamitean tree gradually developed.

In the present article special attention is given to the histological structure and affinities of the genus *Calamites*. Writing of this plant in 1868, Binney[2] draws attention to the desirability of encouraging descriptions and careful examination of our English Carboniferous plants, and adds: "When this is done we are likely to possess a literature on our Carboniferous fossils worthy of the first coal-producing country". Since the above words were penned much has been done towards the realisation of this desideratum; Professor Williamson's series of memoirs "On the Organisation of the Fossil Plants of the Coal Measures"[3] has furnished us with the necessary data from which to build up a fairly complete description of many types of Carboniferous plants. In February, 1894, a paper was

[1] Williamson and Scott, pp. 919 *et seq.*

[2] P. 1.

[3] *Phil. Trans.*, 1871-1893.

read before the Royal Society by Williamson and Scott, on the genera *Calamites*, *Calamostachys* and *Sphenophyllum*. In a prefatory note to this memoir, Professor Williamson writes in the following words: "My morphological inquiries seem to have reached a stage that makes a more minutely careful examination of these questions of development and growth desirable; but before specially undertaking this, I saw clearly the extreme importance of doing so in combination with some younger colleague whose familiarity with the details of the physiology of living plants was greater than my own. Under these circumstances I have secured the co-operation of Dr. D. H. Scott, and the present paper embodies the results of our united investigations." This first instalment under the joint authorship gives an extremely lucid and thorough description of *Calamites* and *Sphenophyllum*, and in addition to working into a complete whole the scattered contributions by Williamson and others on the morphology of these plants, there are several new and important facts embodied in the memoir, which is illustrated partly by photographs, and partly by a series of admirable camera lucida drawings by Mr. Brebner.

The Calamite, as usually found in Upper Carboniferous shales and sandstones, occurs in the form of straight or curved and tapered specimens, with regular transverse constrictions marking the position of the nodes; the internodes are traversed by longitudinal ribs and narrow grooves which generally alternate in position from one node to the next. In most specimens there is a small oval or round protuberance at the upper end of each internodal ridge, giving the appearance of a series of small scars immediately below each node. These are the casts of the "infranodal canals" of Williamson; by some writers regarded as the points of attachment of leaves or roots, but now usually interpreted as the casts of canal-like spaces which extended through the primary medullary ray tissue of the plant. A specimen figured by Williamson in 1878[1] shows the tapered

[1] Williamson (3), pl. xxi., fig. 31.

end of a small cast lying in a cavity, and from the upper ends of some of the internodal ridges small sandstone spokes radiate across the space, and abut on the enclosing face of rock. These rays are simply the slender casts of the infranodal canals, which have been preserved in an unusually perfect form, while the woody tissue which originally occupied the cavity has been entirely destroyed. In addition to these subnodal scars, one occasionally sees in the nodal region of a calamitean cast small dot-like markings representing the place of origin of the leaf-trace bundles; also comparatively large circular depressions on the nodal line; these are the scars of branches. The late Professor Weiss[1] of Berlin some time ago suggested a convenient classification of calamitean casts based on the manner of occurrence of such branch scars. Corda, Dawes and other earlier writers recognised that the specimens of Calamites usually met with, were simply the casts of the fistular pith cavity of the original stem. Williamson brought out this point in a striking manner in the first of his Royal Society memoirs, published in 1891.[2] Stur, in his elaborate work on "Die Calamarien der Carbon-Flora der Schatzlarer Schichten," describes and figures several silicifiel stems from Neu-Paka in Bohemia, in which the true nature of the common casts is clearly demonstrated.[3] In some of these specimens a considerable thickness of wood is preserved, the axis of the stem being occupied by a cavity, the wall of which is formed by the inner face of the wood. This central cavity is partially bridged across at the nodes by the remains of a nodal diaphragm. A cast made of this axial space gives an exact representation of the ordinary calamitean fossil. The examination of sections of a Calamite stem with its woody tissue preserved, shows that the inner face of the wood consists of projecting blunt apices of xylem bundles, separated by broad medullary rays of parenchyma. The thin-walled tissues of the latter would decay more rapidly than the lignified tracheids of

[1] Weiss (2), p. 55. [2] Williamson (2).
[3] Stur, figs. 3-17, pp. 24-37.

the wood, and thus there would be left a series of ribs projecting into the pith cavity. Sand or mud filling up the hollow pith would be moulded on to the surface of the woody ribs and intervening depressions in the primary medullary rays, and thus the surface of the pith cast would present the appearance of narrow grooves alternating with broader ridges.

Our knowledge of the internal structure of *Calamites* is chiefly derived from the minute examination of fragments of small twigs or branches preserved in the calcareous coal balls of Lancashire and Yorkshire, and from the investigations of French palæobotanists, founded on similar fragments from the siliceous nodules of Autun and other districts. When Adolphe Brongniart realised the fact that such Coal-Measure plants as *Calamites* and *Sigillaria* increased in thickness, in a manner strictly comparable to the growth of phanerogamous stems and roots, he was not unnaturally led to look upon the discovery as a fatal objection to these genera being included among the Vascular Cryptogams. He accordingly separated the *Calamarieæ* into two distinct groups: the *Calamiteæ*, closely allied to the *Equisetaceæ*, and the *Calamodendreæ*, included in the Gymnosperms on account of their secondary growth in thickness.[1] This twofold division of calamitean plants was adopted by most writers, and is still retained by one or two French authors. Since Brongniart's time it has been established that secondary growth in thickness does not in itself afford a satisfactory basis of classification. At the present day such a manner of growth is exceptional among Vascular Cryptogams; in such forms as it exists it is only on a small scale; but we have in this circumstance simply an illustration of the methods of development and altered conditions in the vegetable kingdom. In the vast forest which in Coal-Measure times stretched over wide areas reclaimed from the Carboniferous sea, the most abundant and conspicuous trees were arborescent Pteridophytes; with these were associated a few gymnospermous types, but we have abso-

[1] Williamson (4).

lately no evidence that Angiosperms were represented in the vegetation of the Palæozoic Era. Now, on the other hand, the Angiosperms share with the Gymnosperms the making of our forests, and with the exception of some ferns, the Vascular Cryptogams are to a large extent small herbaceous plants clinging as epiphytes to the stems of phanerogams or tree-ferns, or growing in the shade of larger trees. In the Palæozoic forests Calamites, Lepidodendrons and other genera had to struggle upwards for the light, and like the contemporary Gymnosperms or later Dicotyledons, they possessed a power of growth which placed them on a comparatively equal footing with the more highly differentiated forest trees. The difference in size and habit of life between the Palæozoic and recent lycopodinous and equisetinous plants, becomes in some measure less striking when we bear in mind the fact that the trees which predominated in the coal period vegetation have since assumed a secondary importance, and have been replaced by plants which are the outcome of other lines of development, and have usurped the position formerly occupied by types on a lower plane of organisation.

In the recent paper by Williamson and Scott the generic name *Calamites* is used in the wide sense, including *Calamodendron* and *Calamites* of other authors. It may be noted in passing that in Binney's important contribution to our knowledge of calamitean structure in 1868, he adopts the genus *Calamodendron*, but admits that he is unable to recognise any distinct indication of the existence of the two forms of plants insisted on by Brongniart.[1]

It is but rarely that fragments of *Calamites* stems are met with, in which the primary structure has not been added to by the formation of secondary tissues. The greater part of the pith of young twigs is usually hollow, and the regular internal boundary of the parenchymatous tissue suggests an originally fistular stem. The figures of small branches given by Scott and Williamson, and in a recent paper by Hick[2] "On the Primary Structure of the

[1] Binney, p. 16. [2] Hick (2).

Stem of *Calamites*," show a ring of small groups of xylem elements, and in connection with each strand of tracheæ a comparatively large canal. The resemblance of such stems to that of a recent *Equisetum* is exceedingly close, and it is rendered still more real by the occurrence in the carinal canals of fragments of annular, spiral, or more rarely reticulate tracheids. Solms-Laubach,[1] in describing the structure of *Calamites*, suggests that "in the lacunæ, or the tissue that fills them, we are dealing with the tracheal initial strand of the primary bundle"; the observations of Cormack, Scott, Williamson, and Hick have fully confirmed this rational interpretation of these Equisetum-like canals. The nature of the primary xylem structure is admirably shown in an oblique transverse section figured by Williamson and Scott.[2] The phloem of the primary bundle has not been made out in any detail; in describing an exceptionally good section of a young stem, Hick refers to certain small elements external to each canal, "which, from their position and their distinct character, . . . must be regarded as the phloem of the primary bundles";[3] in a longitudinal section these elements are found to have a narrow elongated form. There is no direct evidence of any particular tissue which can be designated a pericycle, nor is it possible to demonstrate satisfactorily the existence of an endodermal layer. Williamson and Scott refer to several specimens in which the innermost cortical layer consists of regular thin-walled cells, fairly distinct from the rest of the tissue, and Hick figures and describes a sharply defined black line passing round the stem in a position suggestive of an endodermis.

The greater part of the cortex of a young branch consists internally of parenchyma, with occasional cells full of carbonaceous matter, and which are probably secretory sacs. Occasionally the more external parts of the cortex are made up of small parenchymatous cells with scattered thick-walled elements, and the outermost layer or epidermis

[1] *Fossil Botany*, p. 298. Oxford, 1891.

[2] Pl. lxxvii., fig. 4.

[3] Hick (2), p. 161.

has been described in one specimen as consisting of a single layer of cells. In the great majority of calamitean stems, of which the internal structure is preserved, we have a greater or less development of secondary wood. The additions to the primary bundles were brought about by the activity of a cambium layer, and, as in a typical dicotyledonous plant, certain cells of the primary medullary rays became meristematic at an early stage of the plant's growth, and gave rise to interfascicular vascular tissue. The secondary xylem consists of radially disposed tracheæ, with scalariform and elliptical pits usually confined to the radial walls. The distribution of the pits is referred to by Williamson and Scott as a fact of considerable interest, "for it indicates that the mechanism for the passage of sap through the wood of *Calamites* was of the same kind as that existing in recent *Coniferæ*".[1] Associated with the tracheæ are regular rows of narrow and thinner-walled elements; these constitute the secondary medullary rays, which increase in number as the result of the production of new rows of ray cells, as we pass outwards through the secondary xylem. In describing the manner of development of the interfascicular wood, the authors of the recent memoir arrive at the conclusion that the interfascicular tracheæ arose "by the elongation of single cells, but that this elongation took place in the cambium cells before the tracheæ were cut off from them".[2] It is extremely rare in the large stems to find any well-preserved cortical tissue; some few examples are known in which a few crushed phloem elements can be detected, and internal to these the remains of thin-walled cambium cells. In the outer part of the cortex strands of stereome fibres are occasionally found, also scattered gum or mucilage sacs. In the early stages of growth in thickness *Calamites* presents a uniform and simple type of structure, but after a time the primary medullary rays show certain differences in their method of growth, which enable us to institute four fairly well-marked types of stem structure. These may be classed as follows :—

[1] Williamson and Scott, p. 882.

[2] *Ibid.*, pp. 886-887.

A. The principal medullary rays remain parenchymatous throughout the whole thickness of the secondary wood. B. The principal rays disappear, as such, towards the exterior, owing to the formation of interfascicular wood.[1]

The retention of Williamson's genus *Calamopitus*[2] is thought advisable in view of the peculiar structure of its medullary rays, and other distinctive features. The type of structure characteristic of *Calamodendron*, as described by Renault and others from France and Saxony, has not so far been discovered in England.

Turning to longitudinal sections, we find many important facts as regards the course of the xylem strands and their behaviour at the nodes. The course of the bundles "is essentially that of *Equisetum*. If we trace any bundle from below upwards, we find that at the node it bends out in a horizontal direction, forming the foliar bundle, which is therefore cut transversely in a tangential direction."[3] At each node the numerous anastomosing bundles form a prominent mass of nodal xylem, which is seen to arch inwards towards the diaphragms; it consists largely of short scalariform tracheæ, and internally of the innermost elements of the primary xylem. The diaphragms uniting the nodal wood across the fistular pith consist of parenchymatous cells, in which there occur distinct traces of meristematic divisions parallel to the upper and lower surface, suggesting the formation of corky tissue. It would appear that the elements of the xylem are tracheids, and not vessels, each being developed from a single mother-cell. In looking at a tangential section through the secondary wood in the neighbourhood of a node, one sees alternating strands of xylem tracheids and comparatively broad primary medullary rays; at the nodes the former bifurcate and fuse with the branches of strands below the node. The upper ends of the rays immediately below a node show fairly clearly a well-defined group of smaller isodiametric cells, some of which may have thickened walls. These infranodal patches of the ray tissues

[1] Williamson and Scott, p. 878.

[2] Williamson (1). [3] Williamson and Scott, p. 875.

frequently became disorganised, leading to the formation of the infranodal canals, of which mention has already been made in reference to the markings on the surface of a medullary cast.

Some few sections of stems show a periderm developed in the inner region of the cortex; the beginnings of such a secondary tissue formation appear in the form of thin tangential walls in certain cells of the primary cortex.

Among structureless specimens of *Calamites*, it is a matter of common occurrence for one end of a medullary cast to taper somewhat rapidly to a point, at the same time being slightly curved and showing a considerable decrease in the length of the internodes. Such examples are casts of the medullary cavity of branches, the pith of which was in organic connection with the pith of an axis of higher order; the place of insertion of the branch being seen as a shallow circular depression on the nodal line. In the Owens College Museum, Manchester, there is a particularly good specimen, showing three such tapered casts in contact with the nodes of a stem. A tangential section through the wood of an axis bearing branches, shows that the latter are given off immediately above the nodes; the basal portion of a branch which is cut through on its way out from the parent stem, presents the appearance of a calamitean axis with a parenchymatous pith, sometimes fistular, surrounded by a ring of collateral bundles. At the actual base of a branch, the internodal canals are absent, but somewhat above the inner extremity there is usually noticed a small gap in connection with each xylem bundle. In these spaces there have been found protoxylem elements, among the thin-walled cells which generally occupy each lacuna, thus enabling us to recognise in these spaces the homologues of the carinal canals of ordinary stems. In certain cases the branches appear to have become abortive; this is rendered highly probable by the peculiar structure occasionally seen in a transversely cut axis, on its way through the parent stem. Such abortive branches became subsequently enclosed by a kind of callus wood, developed by the activity of a meristem layer, formed across the region of the pith. The branches

of *Calamites* were probably developed in a manner precisely similar to that in *Equisetum*.

Some years ago Williamson figured and described several sections of well-preserved axes, showing a distinct resemblance to calamitean stems, but differing, as regards the structure of the wood, in the absence of carinal canals. These he at first regarded as some form of *Calamites*,[1] but subsequently transferred them to a new genus *Astromyelon*.[2] That the earlier opinion was correct has been since demonstrated by the discovery of French silicified specimens, in which an *Astromyelon* axis occurs in direct continuity with a *Calamites* stem, and has been shown to be the adventitious root of that genus.[3] In young examples of this root there have been recognised alternate strands of xylem and phloem, the tracheids showing a distinct centripetal manner of development characteristic of root structures. The secondary wood agrees closely with that of the stem. A constant feature of the cortex is its lacunar zone; there appears to be evidence of the existence of a double endodermis, also a protective epidermoidal layer immediately internal to the epidermis.[4]

In a recent work by Renault, of which plates were published some months ago, but unfortunately without any accompanying text, there are several excellent figures of these adventitious roots of *Calamites*, spoken of in the explanation of the figures as "stolons" of *Arthropitys*.[5] The numerous specimens of *Calamites* represented in this volume lead us to look forward with particular interest to the appearance of the descriptive text.

Among the plants of the Coal Measures there are frequently found long and narrow strobili made up of a central axis bearing verticils of linear leaves. Many of these have been classified by Weiss, and referred to different provisional

[1] Williamson (1), pl. xxv., fig. 16.

[2] *Ibid.* (3), p. 319. [3] Renault.

[4] A full description of these roots may be looked for in a forthcoming paper by Williamson and Scott.

[5] Renault, pl. lvi., etc.

genera. Several are commonly regarded as distinctly calamitean in affinity, but it is nearly always impossible to speak definitely as to the nature of the plant to which they belonged.[1] One of these cones has been known for some time as *Calamostachys Binneyana* Schimp. A recent re-examination of this species, in which the histological structure is very clearly present, has led Hick,[2] and Scott and Williamson to the conclusion that it is most probably a strobilus of some form of *Calamites*, thus confirming the views expressed by Carruthers in 1867. Its structure may be briefly summarised as follows: a slender axis traversed by a stele consisting of a pith surrounded by a ring of bundles, the persistent central tissue consisting of thick-walled cells in the peripheral portion, and thinner-walled elements in the centre. In some cases the central cylinder is triangular in form, in others quadrangular. The position of the protoxylem elements is marked by somewhat irregular spaces; the bundles are of the collateral type, and frequently secondary fascicular and interfascicular xylem has been added to the primary bundles. The cortical tissue consists of thick-walled cells towards the periphery, and more delicate cells internally. Attached to this central axis, which it should be noted shows a distinct calamitean type of structure at the nodes, there are numerous alternating whorls of sterile and fertile lateral appendages, the former being spoken of as bracts, the latter as sporangiophores. Each whorl of bracts is made up of about twelve segments adherent basally in the form of a disk, which is split up at its margin into separate linear segments turned sharply upwards at right angles to the undivided basal portion. Each linear segment is traversed by a small vascular strand. The sporangiophores forming the fertile verticils are usually half as numerous as the bracts; each consists of a pedicel, terminating distally in a peltate expansion, and bearing four sporangia containing numerous spores, often grouped together in tetrads. This form of cone appears to be always homosporous. Each pedicel contains a single bundle,

[1] Weiss (1). [2] Hick (1).

which ultimately breaks up into four branches to supply the sporangia. A fact of special interest in connection with the spores, is the frequent occurrence of feebly developed sister-cells. Speaking of this, Williamson and Scott suggest that in these small spores we have "the beginning of spore-abortion, involving improved nutrition of the surviving spores". In another form of *Calamostachys*, *C. Casheana* Will., "the same process, carried further in certain sporangia, has led to the formation of specially favoured macrospores"; these facts point to *Calamostachys* as "a genus in which the first rise of the phenomenon of heterospory can be traced".[1]

In 1887[2] Williamson described a strobilus with a typical calamitean axis as "the true fructification of *Calamites*".[3] This has since been named *Calamites pedunculatus* Will. and Scott. In assigning a specific name to this cone it would, perhaps, have been better to draw up a concise specific diagnosis; as it is, one is left to formulate a definition from the published figures and descriptions. In this strobilus the sporangiophores are borne at the base of the coherent bracts or disks, conforming in this respect to Weiss' type *Palæostachya;* each sporangiophore bore four sporangia, but no peltate expansion has been seen in the specimens hitherto examined.[4]

Having attempted this very brief and imperfect summary of *Calamites*, we may endeavour in the shortest possible manner to answer the question: "How far does *Calamites* agree with *Equisetum* in essential morphological characters?" Putting aside the absence of true secondary thickening in the recent equisetaceous species, the "primary structure, on which in *Calamites* the secondary zone is superposed, is almost

[1] Williamson and Scott, p. 911.

[2] This form of cone was first described by Williamson in 1869, but the specimens were much less complete than those figured in the later paper (1887).

[3] Williamson (5).

[4] Another form of Calamostachys has recently been described by Hick and Lomax, and named by them *C. oldhamia* (*Manchester Lit. and Phil. Mem. and Proc.*, p. 1, 1894).

identical in the two genera".[1] In *Calamites* the leaves were separate; in *Equisetum* they cohere to form a sheath; in both genera the position of the branches is the same. In *Calamites* the vascular bundles do not always alternate at the nodes as in *Equisetum*, but in their collateral form, and in the character of their elements, the vascular tissue of the two plants is in close agreement. As regards the fructification, one important fact to notice is the occurrence of a heterosporous form of *Calamostachys* (*C. Casheana* Will.); this agrees closely with *C. Binneyana* Schimp, and must probably be included with that species as a calamitean strobilus, differing chiefly in the possession of macrospores and microspores from the cone of a recent *Equisetum*.

It is unfortunate that we are without any information as to the structure of the numerous equisetaceous stems which reached such a large size in the Triassic period; and in the later Jurassic and Wealden rocks still surpassed in the breadth of stem our present representatives of this ancient genus. Without further knowledge of the fossil *Equisetites*, we cannot hope to completely fill up the lacunæ in the records of equisetaceous and calamarian development.

In his later memoirs on Carboniferous plants Professor Williamson made it a rule, in the explanation of plates, to add the number of the page on which each figure was referred to. It would be a great convenience if this custom were continued in the "Further Observations on the Organisation of the Fossil Plants of the Coal Measures," in which new series we may hope to have a succession of memoirs of the highest importance to botanical science.

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THE FORMATION OF LYMPH.

AS the blood circulates through the capillary blood-vessels, some of its liquid constituents exude through the thin walls of these vessels, carrying nutriment to the tissue elements. This exudation is called lymph; it receives from the tissues the products of their activity, and is collected by the lymph channels, which converge to the thoracic duct—the main lymphatic vessel—and thus the lymph once more re-enters the blood stream near to the entrance of the large systemic veins into the right auricle.

Lymph is a fluid which comes into much more intimate relationship with metabolic processes in the tissues than the blood, and the composition and mode of formation of lymph are exceedingly important and interesting physiological questions.

Like most physiological problems it has undergone many vicissitudes. After the disappearance of a belief in a special vital force, Ludwig and his pupils taught that the formation of lymph was a physical process in which filtration played the most important part. There have always been difficulties in the way of a full acceptance of this view, and within recent years Heidenhain has urged that in the normal formation of lymph, filtration plays little or no part; but that lymph is really formed by the selective or secretory activity of the endothelial cells which make up the walls of the capillary blood-vessels. A dictum of this kind supported by exhaustive and careful experiments, coming from a master of his science, was accepted with readiness by a considerable number of physiologists.

It came at a time when with the swing of the pendulum physiologists were beginning to question whether physics and chemistry would, after all, explain all vital problems, and when in consequence a new school of "vitalists" was rising up. Physiological absorption is something else than mere filtration and absorption, and so the view that in lymph formation there is also the vital action of cells to be

reckoned with, fitted in very well with the conceptions of the neo-vitalists.

Although Heidenhain's paper was only published in 1891 there have been numerous researches on the same subject published since. In some of these (*e.g.*, Hamburger's) Heidenhain's views are confirmed, while in other cases (*e.g.*, those of Cohnstein and Starling), Heidenhain's conclusions are disputed, though there is no question as to the validity of his experimental facts.

In the review of this subject that now follows, I propose to deal with these theories of lymph formation, restricting myself, however, to a few of the typical researches, and not attempting to give a *résumé* of all the papers that have appeared. It will be convenient to take this matter in the following order: first to state Ludwig's original position, then rapidly to pass through the various difficulties that stood in the way of the full acceptance of his hypothesis; next to deal rather fully with Heidenhain's epoch-making research, and lastly, to consider the weighty objections that Starling has urged against Heidenhain's views, and which tell in favour of the older idea of Ludwig.

Ludwig[1] speaks of the lymph flow as being conditioned by two factors—first, differences in the pressure of the blood in the capillaries and the fluid in the tissue spaces giving rise to a filtration of fluid through the capillary walls, and secondly, chemical differences between these two fluids, setting up osmotic interchanges through the wall of the blood-vessel. If the lymph is produced by a simple act of filtration, then the amount of lymph must rise and sink with the value of $D-d$, D representing the capillary blood pressure, and d the pressure in the tissue spaces.

In support of this mechanical theory, various workers in the Leipzig laboratory showed (1) that increased capillary pressure, due to obstruction of the venous outflow, increases the amount of lymph formed; (2) that diminution of the pressure in the lymph spaces, by squeezing out the lymph previously contained in them, led to an increase in the transudation. On the other hand, active hyperæmia was

[1] *Lehrbuch der Physiologie*, Bd. ii., p. 562 (2nd edit., 1861).

not found to increase the flow of lymph in any marked degree (Paschutin,[1] Emminghaus,[2] Rogowicz[3]).

In other researches curare was found to have a specific influence in increasing the lymph flow (Paschutin, Rogowicz), and in others stimulation of certain nerves was found to have a similar effect (Ostroumoff). These difficulties were differently interpreted by different physiologists, and although such expressions as "changes in the capillary walls," "an active property in the cells of the capillaries," etc., do occur, there was nothing positive. They, however, paved the way to Heidenhain's work,[4] and to the consideration of his paper we can now pass.

Almost all previous experiments had been made on the lymph of the extremities, but Heidenhain performed his researches by observing the amount of lymph coming from the thoracic duct in fasting dogs. A cannula was placed in the thoracic duct, by means of which the lymph was collected. The first series of experiments were those in which mechanical interferences with the circulation were brought about. The aorta was plugged by means of an elastic ball introduced through the right carotid artery. On the mechanical theory one would expect the outflow of lymph to cease or nearly so with the fall of blood pressure that was the result of this procedure. But though the pressure as measured in the crural artery fell nearly to zero, the lymph was found to go on flowing for one or two hours. In the next set of experiments the portal vein was ligatured near the liver; this led to a great hyperæmia of the abdominal organs; while the arterial pressure fell from 100 to 80 mm. of mercury, the quantity of lymph increased about fourfold, and the percentage of proteids in it fell from 6·5 to 4·4 per cent. Simultaneous occlusion of both portal vein and aorta still produced an increased lymph flow. In the third set of experiments the vessel occluded was the inferior vena cava above the diaphragm; the results of this were that the intestines became anæmic, the liver and

[1] *Ludwig's Arbeiten*, 1873, p. 95.
[2] *Ibid.*, p. 396.
[3] *Pflüger's Archiv*, xxxvi., p. 252.
[4] *Ibid.*, xlix., 1891.

kidneys hyperæmic, and the lymph stream (in spite of the fall of pressure in the aorta) began to flow more freely, and its organic constituents became more abundant.

Heidenhain considered that these experiments indicate that filtration cannot be the main factor in the production of lymph from the blood stream.

In the latter part of his research, to which we now come, an entirely different set of experiments supported this conclusion. He follows up the suggestion originally made by Rogowicz that substances exist which, like curare, have a specific action in increasing the transudation from the blood-vessels, just as diuretics increase the secretion of urine from the kidney. To this class of substances he has given the name of lymphagogues; and these he further divides into two classes. The first class cause an increased flow of more concentrated lymph; the plasma of the blood is diminished in quantity and the amount of solids it contains is also lessened. Long-continued obstruction of the aorta annuls their action from injury to the secretory endothelium of the abdominal vessels. The increased lymph flow is derived from the blood. It may be called "blood lymph". In the greater number of cases the chemical constitution of these substances is unknown, and the materials are most diverse, consisting of extracts of muscles of crabs and crayfish, heads and bodies of leeches, mussels, dog's liver, peptone, and egg albumin. These substances are supposed to stimulate the activity of the secreting endothelium of the blood-vessels.

The second class of lymphagogues contains, on the other hand, such well-characterised chemical substances as grape sugar, common salt, urea and other crystalloids. These increase the lymph flow, but the lymph becomes more watery than before. The blood at the same time becomes also more watery, so that the excess of lymph cannot be derived from the blood, but must come from the tissues. It may be termed "tissue lymph". Diuresis precedes and accompanies the increased lymph flow. In the case of these lymphagogues a physical explanation will in part, but not wholly, explain the phenomena; the substances rapidly diffuse out

from the blood into the lymph spaces, and when there attract water from the tissues. Long-continued obstruction of the aorta does not annul their action. When the aorta is closed for over an hour, injection of crab extract fails to produce a formation or secretion of lymph; but thirty or forty grains of sugar cause at once an increased lymph stream.

From these experiments, Heidenhain distinguishes between the two kinds of lymph, "blood lymph" and "tissue lymph"; he regards the capillary wall not merely as a passive membrane or filter, but one capable of exerting secretory or selective activity, just as the renal epithelium selects from the blood the materials it pours into the urine. This secretory action is stimulated by the substances included in his first class of lymphagogues. He, moreover, points out that the outflow of lymph from the thoracic duct is nearly the same whether the aortic pressure is 10 or 100-200 mm. of mercury, and so blood-pressure cannot be an important factor in lymph formation; and though he admits that in venous obstruction an outflow of fluid takes place as a result of filtration, yet he considers in the normal condition filtration plays no part whatever. This view he founds chiefly on the action of his lymphagogues, which increase the amount of lymph to a marvellous degree, without a corresponding alteration in arterial blood pressure, and the chemical composition of the lymph so formed is incompatible with any mechanical theory; for instance, after the injection of sugar, the percentage of sugar in the lymph rises considerably over that in the blood.

Such then are the main features of a piece of work which has, during the last few years, exercised such a profound influence on the conceptions of modern physiology.

As previously stated, it will be my duty in conclusion to give a *résumé* of the work which Starling has done, and which has led him to oppose Heidenhain's conclusions. The papers he has written are four in number, and they have all been published in the *Journal of Physiology*.[1]

[1] Vol. xiv., p. 131; vol. xvi. (with W. M. Bayliss), p. 159; vol. xvi., p. 224; vol. xvii., p. 30.

The first of these papers was the result of work carried out at Breslau under Prof. Heidenhain's own superintendence, and in it he accepts Heidenhain's hypothesis; but further research (embodied in the three succeeding papers), carried out in London, has led him to abandon this in favour of Ludwig's mechanical filtration theory. He, however, concludes his last paper in these words: "I think I ought to emphasise the fact that my experiments are merely a continuation and not a refutation of those of Heidenhain. Not a single experimental result in his paper, but I have been able to confirm. Indeed, to Prof. Heidenhain's work and teaching I am indebted for all the results that I have succeeded in obtaining."

With this preface, it will be next convenient to take Starling's four papers one by one.

The first paper relates to some points in reference to lymphagogues of the first class, peptone being specially selected, as it is a fairly well-characterised chemical substance. The question investigated was whether the stimulus to the endothelial cells lies in the alteration produced in the blood by the injected material, or in the substance actually injected. As peptone was believed to disappear rapidly from the blood after its injection, still leaving the blood, however, in a profoundly altered condition, the solution of the question was attempted in this wise: If the alteration of the blood is the cause of the increased lymph flow, the injection into a dog of a large amount of blood altered by peptone, but containing little or none of this body, should produce a flow of lymph similar to that brought about by a direct introduction of peptone. After preliminary control experiments with the injection of normal blood, the conclusion is drawn that it is the peptone itself that causes the increased flow of lymph. The principal fact made out, however, is this, that peptone may be detected in the blood for a considerable time (two hours) after its injection. This is contrary to the statements of previous observers, who used methods for detecting peptone which are not at all delicate. In fact the chief value of this research was the introduction of a rapid and trustworthy method for detecting proteoses (albumoses)

and peptone in the presence of large quantities of other proteids like albumins and globulins, such as occur in the blood. The method consists in adding to the blood an equal volume of a ten per cent. solution of trichloracetic acid, and filtering. The precipitate consists of the albumins and globulins, the filtrate contains the proteoses and peptones. This method has yielded most valuable results in the hands of subsequent observers, only, as C. J. Martin[1] points out, it is advisable to boil the mixture before filtering, and filter hot, as in the cold proteoses are partly precipitated by this reagent; the precipitate, however, is soluble on heating.

Starling's next paper, written in conjunction with W. M. Bayliss, relates to the subject of capillary pressure. They point out that in Heidenhain's experiments on the relation of lymph formation to blood pressure, the arterial blood pressure is the only factor measured, and is spoken of as if it were synonymous with or varied directly as the capillary pressure. Now this can only be generally true if the vascular system were composed of tubes through which fluid was flowing from an inexhaustible reservoir. But the vascular system is a closed system of tubes with definite capacity, and containing a definite amount of fluid, and between the capillaries and the arterial pressure is situated the peripheral resistance, that is the arterioles, so that unless we are certain that these arterioles do not vary in calibre, it is impossible to say that a rise of arterial pressure will occasion a corresponding rise in the capillaries beyond the peripheral resistance. The venous pressure would be a better measure of capillary pressure, but it is best of all to take simultaneously arterial and venous pressure, that is the pressure on each side of the capillaries, since it is not practicable to measure the capillary pressure directly. Remembering this principle, but without going into the details of the experiments, it will be useful next to glance through the following table, which gives the main conclusions arrived at:—

[1] *Journal of Physiology*, xv., 375.

Procedure Employed.	Capillary Pressure. In Intestines.	In Liver.
Section of spinal cord	Fall	Slight fall
Stimulation of vagus. Cord cut	Large fall	Slight rise
Do. Splanchnics cut	Large fall	Slight rise
Do. Normal	Fall during, rise after excitation	Rise during, normal after excitation
Asphyxia, normal	Slight rise (?) then a gradual fall	Rise till death
Asphyxia, with cord or splanchnics cut	Fall	(?) Probably unaltered
Excitation of splanchnics	Rise after excitation	Slight rise (?) during excitation
Anæmia	Fall	Fall
Plethora and hydræmic plethora	Large rise	Large rise
Simple hydræmia	Unaffected	Unaffected
Obstruction of aorta	Large fall	Either unaffected or a slight rise
Obstruction of inferior vena cava above diaphragm	Unaffected (?)	Very large rise
Obstruction of portal vein	Very large rise	Fall

The last three experiments in the table are those which Heidenhain performed, and it will be seen how fallacious it is to argue that a fall in arterial blood pressure necessarily implies a fall of pressure in all the capillary areas of the body; and Starling devotes his third paper to pressing this point home in special reference to Heidenhain's work, with the result that he regards intra-capillary pressure as the chief factor in lymph production. To take the three experiments just referred to: In obstruction of the aorta the lymph flow still goes on, though in diminished quantity; this is because the capillary pressure in the liver is either unaffected, or undergoes a slight rise, the lymph which continues to flow coming from the liver; in obstruction of the inferior vena cava, the large increase of lymph is due to the very large increase of capillary pressure in the liver, whereas in obstruction of the portal vein the increase is due to rise of capillary pressure in the intestines and other parts of the portal area.

We may here in passing allude to Hamburger's[1] work

[1] *Zeitsch. f. Biol.*, xxx., p. 143 (1893).

on this subject. His experiments made on horses led him to three main conclusions in support of Heidenhain's views :—

1. That the amount of lymph may rise when the arterial pressure is diminished. But, as already pointed out, arterial pressure alone is no measure of intra-capillary pressure.

2. The proportional composition of blood-serum is not the same as that of the lymph produced at the same time.

3. The osmotic pressure of the lymph is higher than that of the blood-plasma.

Starling points out that these two latter arguments lose a good deal of their weight if it is remembered that the amount of lymph obtained is extremely small, and that we do not know what changes it had undergone on its way through the tissues ; it is quite possible it may have taken up excess of salts from the tissue cells ; certainly the metabolic changes in the tissues would increase the osmotic pressure of the lymph that bathes them.

In his last article Starling tackles the important subject of lymphagogues, and here again he considers that just as in the experiments involving mechanical interferences with the circulation, the increase of lymph can be explained by the filtration hypothesis, and that recourse to a theory of lymph secretion is superfluous.

Take the second class of lymphagogues (sugar, etc.) first ; the mechanical explanation of their action is as follows : On their injection into the blood, the osmotic pressure of the circulating fluid is largely increased, and so water is attracted from lymph and tissues into the blood by a process of osmosis until the osmotic pressure of the blood is restored to the normal. A condition of hydræmic plethora is thereby produced, attended with a rise of pressure in the capillaries generally, especially in those of the abdominal viscera, which causes a great increase in the transudation of fluid from the capillaries, and therefore in the lymph flow from the thoracic duct. Heidenhain pointed out that the lymphagogue effect of these substances is proportional to their osmotic pressures, and therefore to the figure obtained by dividing their osmotic co-efficient by their molecular weight. Since the hydræmic plethora must be also proportional to

this amount, it follows that the intra-capillary pressure will be proportional to the same quantity, and thus all the facts can be explained by the filtration hypothesis.

Members of the first class of lymphagogues act injuriously on the endothelial cells of the capillaries, especially in the liver, increasing their permeability; and also on the muscular walls of the blood-vessels, especially in the splanchnic area, producing vascular dilatation, and thirdly on the heart muscle; the increased flow of lymph is thus not a physiological but a pathological occurrence, and is due to the increased permeability of the hepatic capillaries, nearly all of the increased lymph flow being derived from the liver.

It will be remembered that Heidenhain stated that, after long-continued obstruction of the aorta, the first class of lymphagogues no longer produce an increased lymph flow. This Starling finds is perfectly true; but obstruction of the aorta is a very serious proceeding; it causes extreme injury to the vessel walls, such that when the aorta is again released the pressure in the portal vein rises very slowly, and the intestines are found full of a yellow pasty mass, consisting of desquamated epithelium cells; in fact there is here an exquisite example of Cohnheim's experiment in the production of inflammation by anæmia. Thus it is evident why injection of these lymphagogues has no effect after obstruction of the aorta. The endothelium of the vessels is so damaged that it is as impossible to alter its permeability as it would be to kill a dead dog; though, of course, by injection of sugar or any other lymphagogue of the second class the osmotic phenomena still occur, which lead to an increased formation of lymph.

These are the main points in connection with this subject. I have endeavoured to present both sides impartially, and shall not attempt to pronounce which has, in my opinion, the best of the argument. It would indeed be premature to pronounce judgment at present. Heidenhain has not replied to his critics, and we have not, I imagine, heard the last word on the subject by a long way. Indeed, Starling confesses that on one point his position is incomplete, and this is the very point which to me has always seemed the strongest argument in favour of Heidenhain's views. That is that after injection of sugar, etc., the percentage amount of these substances in the lymph from the thoracic duct rises higher than that in the blood plasma. But as another paper is promised on this subject it would be better to leave the matter as it stands for the present.

W. D. Halliburton.